Restoration of forested wetlands: case studies in Michigan and Finland

……Thesis submitted for a M.Sc. degree in Forest Ecology and Management

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Abstract

Forested wetlands throughout the world are valuable habitats; especially in relatively species-poor northern regions, they can be considered biological hotspots. Unfortunately, these areas have been degraded and destroyed. In recent years, however, the biological importance of wetlands has been increasingly recognized, resulting in the desire to restore disturbed habitats or create in place of destroyed ones. Restoration work is taking place across the globe in a diversity of wetland types, and research must be conducted to determine successful techniques. As a result, two studies of the effects of wetland restoration and creation were conducted in forested wetlands in northern Michigan and southern Finland.

In North America, northern white-cedar wetlands have been declining in area, despite attempts to regenerate them. Improved methods for successfully establishing northern white-cedar are needed; as a result, the target of the first study was to determine if creating microtopography could be beneficial for white-cedar recruitment and growth. In northern Europe, spruce swamp forests have become a threatened ecosystem due to extensive drainage for forestry. As part of the restoration of these habitats, i.e. rewetting through ditch blocking, *Sphagnum* mosses are considered to be a critical element to re-establish, and an in-depth analysis of how *Sphagnum* is responding to restoration in spruce swamp forests has not been previously done. As a result, the aim of the second study was to investigate the ecophysiological functioning of *Sphagnum* and feather mosses across a gradient of pristine, drained, and restored boreal spruce swamp forests.

Preface

The two chapters of this thesis are co-authored manuscripts for journal submission.

The manuscript of Chapter 1 was written by Laura Kangas. Data collection, processing, and statistical analyses were conducted by Kangas as well as the creation of figures and tables. Water table data, however, was collected from the field by Micheal Pennington.

Rodney Chimner provided editing assistance and Pennington provided greater detail regarding site construction. Both Chimner and Pennington were instrumental in establishing the study site in 2007–2008.

The manuscript of Chapter 2 was written by Laura Kangas. Data collection, preparation of tables and figures, and PCA and RDA statistical analyses were also done by Kangas.

Liisa Maanavilja was instrumental in establishing the study sites, including installation of monitoring wells. Maanavilja assisted in gathering information used within the site description, provided editing assistance, and created Figure 2.1.

Tomáš Hájek designed the protocol used for ecophysiological measurements, provided training with equipment operation, offered valuable insight regarding interpretation of ecophysiological parameters, and provided editing assistance. Eija Juurola also assisted in developing the protocol and interpretation of ecophysiological parameters.

Lauri Mehtätalo performed the non-linear and linear statistical analyses and wrote methodology for the non-linear analysis in Materials and Methods.

Eeva-Stiina Tuittila contributed to the non-linear statistical analyses as well as providing editing assistance and statistical support with RDA and PCA.

Rodney Chimner provided editing assistance.

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Chapter 1: Introduction

1.1 History of wetland use

Wetlands have been actively used by humans for centuries for a multitude of purposes. While some uses of wetlands have been relatively sustainable, in many cases these ecosystems have been subject to drainage or other damage for such uses as urban development, agriculture, forestry, and peat harvesting (Dugan 1993). Before the late 1960s/mid 1970s, the practice of draining and/or destroying wetlands has been an accepted practice worldwide and in many cases was even encouraged by government policies (Lappalainen 1996a, Mitsch and Gosselink 2007).

It has been estimated that approximately 50% of the world's original wetland area has been lost (Dugan 1993). This is reflected in focal areas of this research, with 53% drainage in the United States (Dahl 1990), as well as the state of Michigan with 50% loss (Lappalainen 1996b). Countries in northern Europe, notably Finland and Sweden, have lost over 60% of original wetland area (Päivänen 1991, Revenga et al. 2000).

Agriculture has been a tremendous driver for wetland drainage worldwide (Dugan 1993). In northern Europe, however, agriculture has played a smaller role; instead wetlands have been primarily drained to promote the growth of trees for forestry. In Finland, over half of the original peatland area has been drained for forestry alone (Päivänen 1991). In addition to drainage for these uses, road construction can negatively impact wetlands through intercepting the flow of ground water. Altered hydrology often results in sites being too wet or too dry to support the functions of the original habitat type, notably in forested wetlands (Kusler 2006).

1.2 Restoration of degraded wetlands

The aim of wetland restoration is to return a disturbed system to some pre-existing condition. As returning a wetland to original historical conditions is rarely possible, restoration may instead be used to recover a natural range of ecosystem structure (species composition) and function (i.e. hydrology and nutrient cycling) (Palmer et al. 2006). This practice has been gaining interest in recent years with increased knowledge of wetland values. The first organized worldwide initiative for the

conservation and wise use of wetlands began in the 1970s, when the 1971 Ramsar Convention resulted in the signature of an international wetlands treaty (Mitsch and Gosselink 2007).

In the United States, compensatory mitigation has been an important driver for wetland management. The "No Net Loss" policy, which was enacted in 1988 (National Wetlands Policy Forum 1988), mandated no net decline in acreage of the remaining U.S. wetland land base. As a result, creation of new wetlands or restoration of existing wetlands is frequently required for wetland impacts. While wetland restoration is the practice of returning a disturbed or degraded wetland back to some pre-existing condition, wetland creation is the practice of converting upland habitat or a shallow water area into a wetland (Bradshaw 1996).

Practices used for restoration or creation vary depending on the wetland type, and advances in scientific knowledge vary. For example, knowledge of restoring or creating marshes for the benefit of waterfowl and wildlife habitat is well advanced and frequently done (Kusler and Kentula 1989). In both North America and Europe, restoration of peatlands mined for energy or horticultural use has been increasingly studied and practiced (Rochefort and Price 2003, Vasander et al. 2003). The restoration of forested wetlands on the other hand, the focus of this thesis, has been studied and practiced to a much lesser degree, both in Europe and North America.

In an analysis of the status of restoration in the United States, Kusler and Kentula (1989) have considered forested wetlands to be among the most difficult wetland types to restore. The establishment of adequate hydrology is the key requirement for wetland restoration or creation success. However, it is considered more difficult to attain suitable hydrologic conditions in forested wetlands, both for the survival and health of seedlings and the long-term viability of mature trees (Kulser and Kentola 1989, McLeod 2000). This challenge is also presented in northern Europe in the restoration of drained forested peatlands, including in boreal spruce swamp forests, the habitat focused on in the second chapter of this thesis.

1.3 Evaluating wetland restoration/creation success

By studying characteristics of natural wetlands, methods of restoration can be developed to give a better chance of a successful result. Restoration methods can also be improved through evaluating the effects of previous projects to learn for projects in the future. The work presented in this thesis focuses on the restoration/creation of two different forested wetland types in Michigan, USA and southern Finland.

The first chapter of this thesis, *Artificial microtopography and deer herbivory influence* Thuja occidentalis *survival and height in created wetlands,* discusses how characteristics of natural northern white-cedar swamps were incorporated into wetland creation techniques. The paper then discusses the status of the created wetland two years after establishment.

The second chapter, *Changes in* Sphagnum *and forest moss ecophysiology along successional gradients in drained, restored, and pristine boreal spruce swamp forests*, discusses the effects of land use change (drainage and restoration) in boreal spruce swamp forests on the functioning of Sphagnum and forest mosses.

Chapter 2: Artificial microtopography and deer herbivory influence *Thuja occidentalis* survival and height in created wetlands[1]

2.1 Abstract

Northern white-cedar (*Thuja occidentalis* L.) wetlands are highly valuable both commercially and as wildlife habitat. However, northern white-cedar forested wetlands are declining in area from forestry activities and development, with mitigation efforts often failing to reproduce these ecosystems. Therefore, the goal of this project was to determine the feasibility of creating a northern white-cedar wetland as a mitigation option. As microtopography has been shown to be important for northern white-cedar establishment and recruitment, a series of hummocks, pools, and flat areas were created and planted with northern white-cedar seedlings and wetland herbaceous seeds from 2007 to 2008 in two created wetlands in northern Michigan. We examined the influence of microtopography and deer browsing on white-cedar survivorship and height and herbaceous vegetation cover. Two years after establishment, microtopography had a strong effect on cedar survival, with hummocks positively affecting survivorship by creating drier microhabitats at wet sites. Tree height was less affected by microtopography. Protection from browsing increased survival and height, although results were not significant in all cases. Microtopography also strongly influenced the partitioning of herbaceous vegetation communities. Our results indicate that incorporating microtopography into future restoration or regeneration projects involving northern white-cedar should be considered as a viable option where high or variable water tables are expected.

[1] The material contained in this chapter is planned for submission to the journal *Ecological Engineering*.

2.2 Introduction

Northern white-cedar (*Thuja occidentalis* L.), a tree native to the northeastern United States and southeastern Canada, is highly valued throughout its range. Its water resistant wood makes it a valuable commercial timber species (Sandberg 1983). Northern white-cedar -dominated lowland conifer swamps are also valuable wildlife habitat, in which over eighty animal species use northern white-cedar throughout the community's successional stages (Doepker and Ozoga 1990). This includes providing important habitat for wintering white-tailed deer herds (*Odocoileus virginianus*,Verme 1965).

However, the area of northern white-cedar wetlands has been steadily decreasing throughout the last half century. In both forestry practices and compensatory mitigation, white-cedar wetlands are being replaced by other habitat types. Compensatory mitigation, often required by federal and state regulations, requires the creation of new wetlands following wetland impacts. However, few successful forested wetlands are being created for mitigation purposes, resulting in forested wetlands being replaced by other wetland types, such as emergent marshes or freshwater ponds (Kusler 2006).

Methods for creating herbaceous wetlands have been well established (Kusler and Kentula 1989), aided by the short time span to achieve vegetative maturity. Forested wetlands, however, require decades to mature, thus making it difficult to evaluate restoration methods (Clewell and Lea 1989, Kusler 2006). In addition, developing the proper hydrologic conditions has been difficult in forested wetlands (Kusler 2006). Even slight differences in elevation can have a large impact on survival and health of seedlings planted in forested wetlands due to differences in water levels (McLeod 2000, Pennington and Walters 2006).

For these reasons, artificially created microtopography has been emerging as an important tool in wetland creation and restoration in recent years (Barry et al. 1996, Bruland and Richardson 2005, Ahn and Dee 2011, Simmons et al. 2011). Microtopography, defined as small-scale topographic variation at the scale of 1 cm to 1 m (Moser et al. 2007), is a common feature of many types of natural wetlands. In

these ecosystems, microtopography is naturally formed through tip-up root mounds, downed trees, differential litter fall and sedimentation, and animal burrowing (Barry et al. 1996, Chimner and Hart 1996, Stolt et al. 2000). Small-scale variations in topography create a number of microhabitats with different water levels, ranging from drier, raised hummocks to flooded pools. As a result, microtopography tends to increase plant species diversity in both natural and created forested wetlands (Vivian-Smith 1997, Kusler 2006). Important to forested wetlands, elevated microforms increase the probability of tree survivorship by providing aerobic growing conditions (Barry et al. 1996, Kusler 2006).

Microtopography can be created through a variety of techniques, including bucket mounding, tire rutting, and disk harrowing (Barry et al. 1996, Moser et al. 2007). Most previous studies have focused on the construction of microtopography in bottomland hardwood swamps, which have shown that the effect of microtopography varies by tree species. Pioneering species adapted to fluctuating water levels and periodic flooding performed better in pools, while improved survival of later-successional species and trees that cannot withstand prolonged flooding were found on hummock tops and ridges (Simmons et al. 2011, 2012).

The use of microtopography, however, has been minimally addressed in the literature involving white-cedar restoration or regeneration methods, despite its prevalence in pristine white-cedar swamp ecosystems. While white-cedar commonly grows in moist sites, on organic soils near streams or drainage-ways, growth is impeded on extremely wet sites (Johnston 1990). For this reason, elevated microtopography is an important component in natural northern white-cedar wetlands, especially during the critical stages of germination and seedling establishment.

The presence of microtopography has also been shown to increase white-cedar regeneration under natural conditions, which is an important implication for forestry practices. The declining regeneration of white-cedar is typically attributed to overbrowsing by white-tailed deer, which use white-cedar as a winter food source (Rooney et al. 2002, Forester et al. 2008). However, a lack of proper microsites may also be a factor. In a study of a northern white-cedar stand 30 years following clearcutting (Chimner and Hart 1996), the land area composed of hummock

microtopography was correlated with the densities of white-cedar. While areas with greater than 70% hummock microtopography had the greatest densities of white-cedar, as hummock microtopography decreased in extent, density of white-cedar decreased proportionally, with less topographically diverse areas becoming dominated by shrubs and hardwoods (Chimner and Hart 1996).

Although the use of microtopography appears to be overlooked in white-cedar restoration and regeneration practices, the artificial creation of microtopography has a strong potential for both created and restored northern white-cedar wetlands. This study examined the effects of artificially created microtopography on northern white-cedar growth and herbaceous vegetation patterns in two created forested wetlands. The specific objectives of the study were to determine the influence of microtopography and deer browsing on 1) northern white cedar survival and height, and 2) the distribution and abundance of seeded and naturally-colonizing herbaceous vegetation communities.

2.3 Materials and methods

2.3.1 Study Sites

This study was conducted at two compensatory wetland mitigation sites in northern Michigan, near Petoskey (45° 20.367'N, 84° 55.252'W) and Isabella (45° 53.725'N, 86° 37.553'W). Petoskey has a mean annual precipitation of 791 mm and mean annual temperature of 6.5 °C (NOAA 2002). Isabella has mean annual precipitation of 726 mm and a mean annual temperature of 6.4 °C (NOAA 2002). Prior to wetland construction, 32 soil borings were performed at Petoskey, and 20 soil borings were performed at Isabella. Borings indicated that Petoskey was located on loamy sand, while soils at Isabella were silt loam underlain by sandy clay loam or clay loam. Surface water at Isabella had a pH of 7.26 and specific conductivity of 455 µS, while pH was 7.55 and conductivity 224.5 µS at Petoskey.

In 2007, wetland construction was conducted by the Michigan Department of Transportation at both locations to serve as mitigation for impacts to wetlands within the state of Michigan. Both sites were upland areas prior to wetland construction, and

the Petoskey site was used for grazing and the Isabella site used for hay production. In total, 9.3 ha of wetland were constructed in Petoskey and 2.4 ha were constructed in Isabella. Within these areas, small experimental blocks incorporating microtopography and deer browse protection were created at each site.

2.3.2 Experimental design and treatments

At each site, six experimental blocks were created to form a complex of hummocks, flats, and pools (Figure 2.1). Topsoil was stripped from the site and stockpiled, and the site was graded topographically flat to a level 15 cm below the final elevation of the flat surface. On top of the sub-grade, hummocks were created with an excavator by placing buckets of topsoil individually for each mound (Figure 2.2). On the flats outside of the hummock complexes, topsoil was replaced to a depth of 15 cm. Pools are defined as the area between each hummock below the average elevation of the flats.

At Petoskey, 90 hummocks were constructed in each block. At Isabella, 78-116 hummocks were constructed per block, with an average of 96 hummocks per block. Hummock tops were approximately 50 cm higher than pool bottoms in Petoskey and 25 cm higher than pool bottoms in Isabella (Figure 2.1). Resulting hummocks were approximately 1.5 m in width at Petoskey and 1 m wide in Isabella, measured at the elevation of the flats. Each hummock and pool complex was surrounded by a large topographically flat area.

Adjustable water control structures also were incorporated into the design at both sites. At both sites, the stop logs of the water control structure were set at the elevation of the flat surface, allowing excess water to run off the site in spring. After the sites were planted, water control structures were not adjusted to manipulate water levels.

2.3.3 Cedar planting

In the spring of 2008, northern white-cedar seedlings were planted on each hummock top and on flats; no seedlings were planted in pools. On flats, seedlings were planted at approximately 2.8 m x 2.8 m spacing, with 90 seedlings per block in Petoskey and 39-84 seedlings per block in Isabella (average 63 seedlings/block). Hummocks and

flats had an average of 1340 trees/ha in Petoskey and 1220 trees/ha in Isabella. White-cedar seedlings were bareroot-planted. At time of final planting, seedlings were 15-30 cm in height at Petoskey and 30-45 cm at Isabella.

In Petoskey, fencing was established around half of each block to prevent deer browsing, resulting in four treatment types: fenced hummock, fenced flat, non-fenced hummock, and non-fenced flat. Each treatment contained 45 seedlings. Only two blocks contained the non-fenced flat treatment.

At Isabella, treatments were unbalanced due to improper fence placement. Only two blocks included non-fenced hummocks (trees per block = 6 and 30) and 3 blocks contained fenced flats (trees per block = 5, 8, and 10). The fenced hummock treatment contained 78-106 seedlings per block and non-fenced flats contained 31-80 seedlings per block.

A wetland herbaceous seed mix was broadcasted at each mitigation site, including 23 species in Petoskey (8 forb and 15 graminoid species) and 30 species in Isabella (12 forb and 18 graminoid species). The Petoskey site was seeded in the fall of 2007, while Isabella was seeded in the spring of 2008. Species included in the seed mixes are indicated by an asterisk (*) in Appendix A, Table A.1 and A.2.

2.3.4 Vegetation Sampling

All northern white-cedar trees were assessed for survivorship and total height in April 2010, two years after planting. Herbaceous vegetation sampling was conducted in July 2010. In Petoskey, 18 subplots were sampled per block, with 6 subplots in each microtopography type (hummock, pool, lawn) randomly selected equally both in and outside of the fenced enclosure. At Isabella, 3 subplots each of hummocks and pools were sampled per block and only within the enclosures using the same methods. Quadrat size was 1 m^2, and centered over the selected microform. All herbaceous and woody plants were identified to species, with percent cover assigned by cover class (6 class intervals: <1%, 0-5, 6-25, 26-50, 51-75, 76-100%). The midpoint within each cover class was used for analysis.

Herbaceous species were classified by Region 3 (North Central) wetland indicator status for general comparison across microtopography type: obligate wetland plants

(OBL) occur in wetlands 99% of the time, facultative wetland species (FACW) occur in wetlands 67%-99% of the time, facultative species (FAC) occur in wetlands 34%-66% of the time, facultative upland species (FACU) occur in wetlands 1%-33% of the time, and upland species (UPL) occur in wetlands less than 1% of the time (U.S. Fish and Wildlife Service 1988, U.S. Fish and Wildlife Service 1993, USDA NRCS 2011). OBL, FACW, and FAC species are considered wetland species (MDEQ 2003).

2.3.5 Soil and Hydrology Sampling

Soil sampling was conducted in July 2010. In Petoskey, 18 soil samples were collected per block with 6 subplots from each microtopography type (hummock, flat, and pool) randomly selected equally both in and outside of the fenced enclosure. Soil samples were taken from the center of microform. At Isabella, 6 soil samples were collected per block, from three subplots each of hummocks and flats. Due to the fencing design in Isabella, hummocks were sampled from within the enclosures, and samples from flats were taken from outside the enclosure.

Soil bulk density cores were collected using a 71.5 cm^3 cylinder (5 cm diameter) from the upper 1–5 cm soil surface of hummocks and flats. Soils were stored in polyethylene bags and frozen until laboratory analysis. Samples were oven-dried at 105°C for 24 hrs to determine dry weight and sieved to remove material greater than 2.0 mm. Bulk density was calculated from soil dry weight divided by the core volume (Elliot et al. 1999).

For all microtopography types, dried soil was used to determine the percent soil organic matter by loss-on-ignition for 4 hrs at 500˚C (Storer 1984) and soil texture was determined using the hydrometer method (Bouyoucos 1962). At Petoskey, soil texture analysis was done only for fenced subplots.

Depth of water table was measured at three wells per site, using Ecotone WM 1.0m water level monitors (Remote Data Systems, North Carolina, USA) that took one reading daily. Wells were installed in November 2007 in Petoskey and June 2008 in Isabella and were located to capture the range of water levels encountered at each site.

2.3.6 Statistical Analyses

To determine differences in tree height due to microtopography type (hummock and flat), fencing, and microtopography × fencing interactions, a mixed model ANOVA was used (SAS, PROC MIXED), with block and block x fence as random factors according to the model for a split-plot randomized complete block design (Littell et al. 2006). To determine effects on survival, the percentage of live trees at each block was calculated for all treatment combinations. Percent survival data were normalized using the arcsine square-root transformation (Steel and Torrie 1980) and analyzed using ANOVA with microtopography, fencing, and the microtopography × fence interaction as the main effects (PROC GLM). Specific differences across treatments were determined using Tukey's post-hoc test. Statistical analyses were done separately for each site due to differences in site hydrology and soils.

To determine differences in herbaceous cover and percent cover of planted species due to microtopography type (hummock, flat, and pool), fencing, and microtopography x fencing interactions, a mixed model ANOVA was used according to the model for a split-plot randomized complete block design, with block and block × fence as random factors (Littell et al. 2006). Specific differences across treatments were determined using Tukey's post-hoc test.

Abiotic characteristics (bulk density, soil organic matter, and soil texture) were only tested across microtopography type. As a result, a mixed model ANOVA, with block as the random factor, was used to examine differences in microtopography type, according to the randomized complete block design (Littell et al. 2006). Specific differences across microtopography type was determined using Tukey's post-hoc test. Statistical analyses were done using SAS for Windows version 9.1 (SAS Institute, Cary, NC, U.S.A.)

2.4 Results

2.4.1 Soil and hydrologic properties

Both sites are characterized by highly fluctuating water levels. Water levels were on average higher in Petoskey than Isabella over the 2.5 year measurement period (Figure 2.3). In Petoskey and Isabella, the water was above the flat surface for an average of 100 days per year and 60 days per year, respectively, while hummock tops were never inundated at either site. Peak water levels in individual wells reached 25 cm above the flat surface in Petoskey and 20 cm in Isabella.

In Petoskey, organic matter and soil texture differed with microtopography type (Table 2.1). Organic matter was highest in pools and least on flats ($p < 0.001$). Pools contained less sand and more silt and clay compared to hummocks and flats ($p < 0.05$). Bulk density was not affected by microtopography type ($p = 0.17$)

In Isabella, organic matter and bulk density varied with microtopography type, but soil texture did not (Table 2.1). Organic matter was similar between hummocks and pools, but significantly lower on flats ($p < 0.001$). Bulk density was slightly higher on flats than hummocks ($p < 0.01$).

2.4.2 Tree survival and height

Tree survival was positively affected by microtopography and fencing (Figure 2.4), however, differences were significant only at Isabella ($p < 0.01$). In Petoskey, percent survival was significantly higher on hummocks than flats ($p = <0.001$, Figure 2.4a). In Isabella, survival was highest on fenced hummocks, however, it was not significantly different from either fenced flats or non-fenced hummocks (Figure 2.4b). The only significant difference was seen in non-fenced flats, which had lower percent survival than all other treatments ($p < 0.05$). The interaction between microtopography and fencing was significant in Isabella ($p = 0.01$).

The effect of browsing and microtopography on tree height was more pronounced in Isabella (Figure 2.4). In Isabella (Figure 2.4d), height was greatest on fenced hummocks and significantly higher than fenced flats ($p < 0.05$). Combined across microtopography type, all trees protected from browsing were significantly taller than

trees outside fences ($p < 0.05$). At Petoskey, tree height was significantly higher on hummocks than on flats ($p = 0.036$, Figure 2.4c).

2.4.3 Herbaceous Vegetation

In Petoskey, 57 colonizing herbaceous species and 13 planted species were identified in vegetation surveys, with six identified to genus and 62 identified to species. Two taxa could not be identified due to the immature growth stages. Hummocks had the highest species richness, with an average of 14.4 species/m^2, followed by lawns (11.6 species/m^2), and pools (8.4 species/m^2). Hummocks also had the highest species diversity, for both all species and when only considering native species (Table 2.2). Pools contained the greatest number and cover of obligate wetland species, followed by hummocks and lawns. Of the 70 total species, 20 were non-native, with *Agrostis stolonifera* and *Hypericum perforatum* the most common non-native species (Appendix Table A.1).

In Isabella, 59 colonizing herbaceous species and 8 planted species were encountered in the vegetation surveys, as well as 2 tree seedlings. Of the herbaceous species, seven were identified to genus, 58 identified were identified to species, and two taxa could not be identified due to the immature growth stage. Hummocks and pools had similar species richness, with an average of 18.7 species/m^2 on hummocks and 18.2 species/m^2 in pools. Species diversity was also similar between microtopography type; however, when only native species diversity was considered, pools had significantly greater diversity than hummocks ($p = 0.006$, Table 2.2). Pools contained a greater number of obligate wetland species and planted species than hummocks, however, the percent cover of these cover types were higher on hummocks. Of the 67 total species, 16 were non-native, with *Lotus corniculatus* and *Phalaris arundinacea* the most common non-native species (Appendix Table A.2).

2.5 Discussion

2.5.1 Microtopography

Hummock microtopography improved northern white-cedar survival at both sites. As white-cedar is a slow-growing, late-successional species, these results correspond

with the improved survival of late-successional tree species on drier microtopography in bottomland hardwood swamps (Simmons et al. 2011, 2012). Water table appeared to be the dominant environmental driver between hummocks and flats, especially during periods of flooding. Following site construction, there was concern that compaction from the heavy equipment may have occurred on flats, thus making conditions less suitable for tree growth. Measurements of soil bulk density, however, yielded no differences in Petoskey and minimal differences in Isabella (Table 2.1). Significant differences in soil organic matter were found at both sites between hummocks and flats ($p < 0.001$, Table 2.1). Although differences in organic matter were small, during periods of low water levels, increased organic matter could have a positive effect on tree survival. As the most cost effective way for the contractor to construct hummocks was from topsoil only, the average depth of topsoil was deeper on hummocks than on flats. This may have been an additional positive benefit toward seedling survival in addition to protection from flooding.

White-cedar cannot withstand prolonged inundation (Johnston 1990), thus, microtopography functions in elevating seedlings above high water levels. However, the effectiveness of hummocks also varies depending on site hydrology. Hummocks are essential to seedling survival in sites with long periods of standing water, but as the number of days of inundation decreases, hummock microtopography becomes less necessary. This is shown by the results of this study as fenced white-cedar survival averaged less than 4% in wet flats at Petoskey, but averaged 87% on drier flats at Isabella. At Petoskey, the water table was above the surface of the flats for an average of 100 days per year—this high degree of flooding was clearly unsustainable for white-cedar survival on flats, even with the incorporation of the water control structures. This is in comparison to an average of 60 days per year at Isabella, which resulted in a flooding level that could sustain cedar survival on the flat surface. As soil textures varied between the two sites, this may have also had an effect on white-cedar survival, especially during periods of low water levels during the summer months. The sandy loam present in Petoskey results in a lower water holding capacity than the silt loam present in Isabella. As a result, the combination of low organic matter and sandy soils in flats in Petoskey could have had a negative effect on seedlings during droughty conditions.

Acquiring the proper hummock height is necessary for wetland restoration/creation success. The average hummock height at Petoskey was 26 cm above the soil surface and 14 cm above the soil surface in Isabella. These heights range above and below the average hummock height in a natural northern white-cedar swamp (Chimner and Hart 1996), where hummocks had an average of 21 cm in height and 0.5 to 3 m in diameter. Diameters of hummocks in Petoskey and Isabella were 1.5 m and 1 m, respectively. However, the necessary height will vary depending on the specific hydroperiod; a too low hummock may not provide enough protection against high water, whereas a too high hummock may result in excessive drying during low water levels. In this study, with average water levels ranging from -91 cm to 25 cm in Petoskey and -86 cm to 13.7 cm in Isabella, hummock elevations at both sites functioned well when approximately similar to the height of peak water levels. In Petoskey, water control structures played an important role in minimizing sustained high water levels, as excess water was permitted to drain off-site. Lacking the water control structure, even hummocks would have been inundated during high water levels in spring. Water control structures at Isabella played less of an important role due to the lower water levels. As the primary function of hummocks is to elevate trees above high water levels, the height of created hummocks can therefore be decreased for sites with lower water levels or water control structures. However, in this instance, the varying hummock height by site was the result of different contractors conducting the wetland construction, rather than attempting to acquire specific heights based on site hydrology. More work on developing the optimum elevation above the water level is needed for white-cedar on different microforms.

Microtopography was also a strong driver in the development of herbaceous vegetation communities. The effects of microtopography on understory species partitioning has been observed in natural communities (Beaty 1984, Paratley and Fahey 1986), and increasingly has been shown to influence vegetation patterns in created wetlands (Vivian-Smith 1997, Bruland and Richardson 2005, Moser et al. 2007, Rossell et al. 2009, Simmons et al. 2011). In this study, it was expected that most wetland species would occur in pools, and decrease in coverage with increasing elevation. In Petoskey, while this held true for pool microtopography, it was not the case between hummocks and flats, as a significantly greater coverage of obligate

wetland species occurred on the hummocks compared to the flats ($p < 0.001$). Both hummocks and pools had a high cover of native wetland species, corresponding to 96% and 108%, respectively. Flats, however, only supported 54% cover of native wetland species. The differences in species distributions between hummocks and flats are likely to be affected by the spatial distribution of microtopographic types, in which hummocks were surrounded by deep pool microtopography, while flats were spatially separate. Thus, wetland species established in pools would be able to more easily establish on the lower portions of hummocks. Rossell et al. (2009) also observed the colonization of both OBL and FACW species on drier ridge microtopography. Not all site conditions support wetland species on elevated microforms, however, as Bruland et al. (2005) observed very distinct vegetation communities between microforms, in which hummocks did not support any OBL or FACW species. Site hydrology and the relative elevation of the microforms are important drivers toward the differing results.

In Isabella, the drier site conditions, as well as the lower elevation differences between hummocks and pools, resulted in less distinct differences between hummock and pool communities, as hummocks and pools had no significant difference in the coverage of either wetland or facultative upland species ($p = 0.56$ and 0.22, respectively). Hummocks did have, however, significantly greater coverage of species that have not been given a wetland indicator status ($p = 0.04$, USDA NRCS 2011). These non-listed species typically occur in upland habitats (Appendix Table A.2). Although low water levels in Isabella resulted in higher percent survival of white-cedar seedlings, it also resulted in greater coverage of upland herbaceous species.

It was expected that the addition of hummock and pool microtopography to the otherwise flat topography would increase the number and cover of seeded species that established. In Petoskey, ten seeded species were found on flats; the addition of microtopography resulted in three additional species. Percent cover of planted species was lowest on flats (Table 2.2). The greater coverage of planted species in hummocks and pools resulted from a high cover of *Carex vulpinoidea* and *Alisma subcordatum*, respectively. This is in accordance with the theory that greater numbers of microsites

increase the niche availability for a higher richness of species in created wetlands (Vivian-Smith 1997).

Microtopography also had an effect on the diversity of native and non-native species. Hummocks at Petoskey had the highest percent cover of non-native species (53% cover), followed by flats (39%). Due to the greater density of plants on hummocks, the proportion of native to non-native species was the same on hummocks and flats. Cover of non-natives was lowest in pools, with 16%. This trend was followed at Isabella, with 59% cover of non-natives on hummocks and 35% cover in pools. This is also reflected in a higher native diversity in pools in Isabella (Table 2.2).

2.5.2 Fencing and deer browse

Many studies have indicated that regeneration of northern white-cedar is impaired by deer browsing (e.g., Heitzman et al. 1997, Forester et al. 2008). In a Wisconsin study, regeneration was nearly eliminated three years after harvesting in unfenced plots, and tree height was already impacted after one year (Davis et al. 1998). In our study, percent survival and height decreased at both sites when subject to deer browse, but differences were not significant in all cases (Figure 2.4). After two years of growth, white-cedar in our study has already shown signs of decreased health from deer browse. As browsing will likely continue in the future, reoccurring impacts will result in stronger differences between fenced and non-fenced treatments.

Neither height nor survival were affected by browsing on flats in Petoskey. This is likely due to the primary effect of microtopography type and water level, resulting in a very low number of surviving trees (n=8 total surviving trees in flats). The within-site height differences due to browsing protection vary between sites, as the effect of fencing varies with browsing pressure at the site. From field observations of the surrounding area, browsing pressure at Petoskey appeared to be less than Isabella. This is illustrated in the more even height profile across treatments in Petoskey compared with Isabella.

Advisory guidelines have been prepared to guide the establishment of herbivore exclosures for research on northern white-cedar (Miller 1990). However, the high cost associated with fence installation commonly makes this impractical for large-

scale wetland restoration/creation and forest management. Northern white-cedar is a slow-growing tree, and may take up to 40 years for seedlings to grow above deer browsing height (Van Deelen 1999). White-cedar survival at Isabella showed an interesting interaction between fencing and microtopography. Fenced flats exhibited significantly higher survival than those not protected from browsing (87% versus 17%, respectively) (Figure 2.4). However, survival on non-fenced hummocks was not significantly different from fenced hummocks (78% versus 95%, respectively). Created hummock microtopography may increase tree health and resilience, therefore lowering the effects of deer browse in comparison to flats. However, the vigor of non-fenced compared to fenced trees was lower due to repeated browsing, thus decreasing their chance of survival in the longer-term. In addition, the sample sizes of non-fenced hummocks were too small to be conclusive, and these effects were only seen at one site.

Herbaceous vegetation communities were minimally affected by deer browse, although this was only tested in Petoskey due to the sampling design. Browsing did not significantly affect species diversity, and no significant differences were found in herbaceous cover between fenced and non-fenced treatments for all of the species groups presented in Table 2.2. Over-browsing by deer has significantly affected other herbaceous vegetation communities (Cote et al. 2004, Webster et al. 2005). These studies have shown changes in the composition of herbaceous species over time (Cote et al. 2004), especially a decrease in the richness and diversity of spring ephemerals due to deer browsing (Webster et al. 2005). Herbaceous vegetation in this study may not have been impacted by browsing due to the lack of preferential forage species or the short period of time since site establishment.

2.6 Conclusion

Although the strength of the findings in this study is limited due to the low sample sizes, some important conclusions can be made and also provide a direction for future research. For both northern white-cedar regeneration and the creation of forested wetlands for mitigation, using microtopography and controlling water levels can have positive effects on tree survival. Convenience and cost, as well as limited

understanding of natural forested wetland structure, often results in the creation of flat sites in restoration and creation projects. However, this limits the site to a single water table level, where the risk of a low diversity site and mortality of planted seedlings from seasonal high water is high. Microtopography increases niche sites for species, and also provides sites with varying degrees of saturation (Barry et al. 1996). Incorporating microtopography in the creation of lowland hardwood forests in the southern United States has been recommended (Bruland and Richardson 2005, Simmons et al. 2011); the same is recommended here in the creation of northern white-cedar wetlands. The importance is elevated, however, as northern conifers have shown an even greater preference for drier microsites than swamp hardwood species (Chimner and Hart 1996).

Tables

Table 2.1
Soil properties by site and microtopography type analyzed according to mixed-model ANOVA and Tukey's HSD test. Means ± SE (n = 6).

		PETOSKEY		ISABELLA	
		Average ± SE	p-val	Average ± SE	p-val
Organic matter (%)	hummock	3.7 ± 0.11 [a]	**<0.001**	7.7 ± 0.06 [a]	**<0.001**
	lawn	3.0 ± 0.08 [b]		6.4 ± 0.19 [b]	
	pool	4.3 ± 0.27 [c]		7.5 ± 0.17 [a]	
Bulk density (g/cm3)	hummock	1.3 ± 0.02	0.177	1.1 ± 0.02 [a]	**0.003**
	lawn	1.3 ± 0.01		1.2 ± 0.02 [b]	
% Sand	hummock	86.4 ± 0.33 [a]	**0.002**	37.5 ± 2.05	0.854
	lawn	86.4 ± 0.44 [a]		38.6 ± 1.16	
	pool	83.6 ± 0.93 [b]		37.4 ± 1.76	
% Silt	hummock	8.7 ± 0.34 [a]	**0.025**	48.4 ± 1.61	0.782
	lawn	8.7 ± 0.29 [ab]		47.4 ± 1.11	
	pool	10.2 ± 0.62 [b]		47.2 ± 1.39	
% Clay	hummock	4.9 ± 0.24 [a]	**0.026**	14.1 ± 0.68	0.273
	lawn	4.9 ± 0.29 [b]		14.1 ± 0.59	
	pool	6.2 ± 0.54 [b]		15.4 ± 0.74	

Different letters indicate significant differences between microtopography type ($p < 0.05$)

Table 2.2
Results from mixed-model ANOVA and Tukey's HSD test for herbaceous species: total cover of herbaceous vegetation and average percent cover of herbaceous species grouped by wetland indicator status, native status, and planted species across microtopography types. Species totals by wetland indicator and native status are for plants identified to species level; total cover and diversity calculations include unknown plants and plants identified to genus (n = 6).

	PETOSKEY					ISABELLA			
Group	No. of species	Hummock	Flat	Pool	p-value	No. of species	Hummock	Pool	p-value
OBL	24	81.4[a]	39.2[b]	123.2[c]	**<0.001**	15	24.4	21.4	0.562
FACW	10	34.3[a]	36.2[a]	0.7[b]	**<0.001**	14	45.9	34.8	0.055
FAC	15	10.4[a]	15.7[a]	0.6[b]	**<0.001**	13	38.6[a]	20.1[b]	**<0.001**
FACU	8	1.4[a]	4.7[b]	0.1[a]	**<0.001**	9	5.3	2.6	0.222
not listed	5	24.8[a]	1.4[b]	0[b]	**<0.001**	7	14.1[a]	7.8[b]	**0.040**
Introduced	20	53.4[a]	38.7[a]	16.0[b]	**<0.001**	16	59.0[a]	35.4[b]	**0.001**
Native	42	96.1[a]	57.1[b]	108.6[a]	**<0.001**	42	69.4[a]	50.8[b]	**0.040**
Planted	13	40.1	34.7	44.7	0.156	8	23.9	20.8	0.554
Total cover	70	167.0[a]	117.8[b]	142.0[c]	**<0.001**	67	131.5[a]	89.0[b]	**<0.001**
Diversity	-	1.79[a]	1.35[b]	1.47[b]	**<0.001**	-	1.89	2	0.233
Native diversity	-	1.39	1.3	1.23	0.109	-	1.23[a]	1.51[b]	**0.006**

Figures

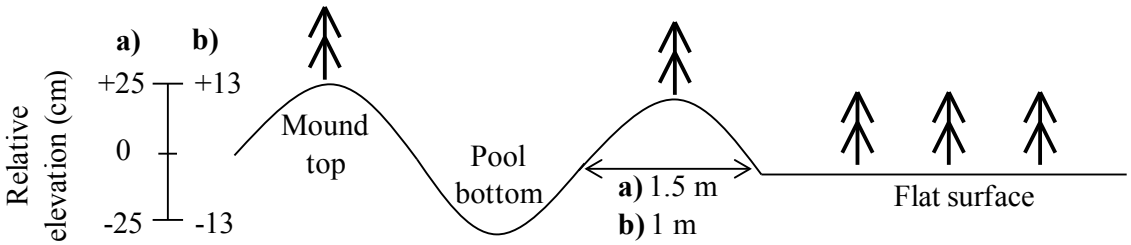

Figure 2.1 Illustration of hummock, flat, and pool microtopography at Petoskey (scale a) and Isabella (scale b).

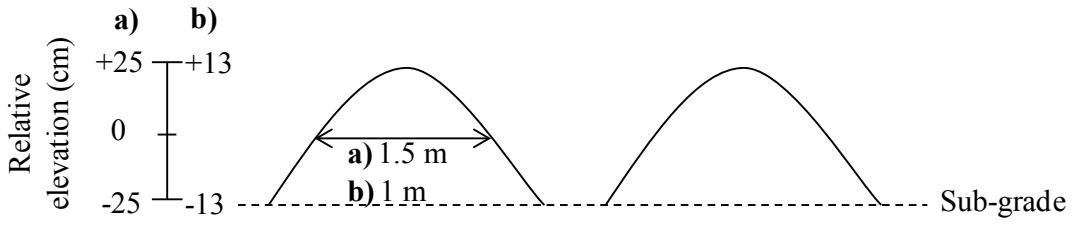

Figure 2.2 Diagram of hummock construction before the topsoil has been replaced on the sub-grade of the flat surfaces surrounding the hummock complexes (Scale bars a and b represent Petoskey and Isabella, respectively).

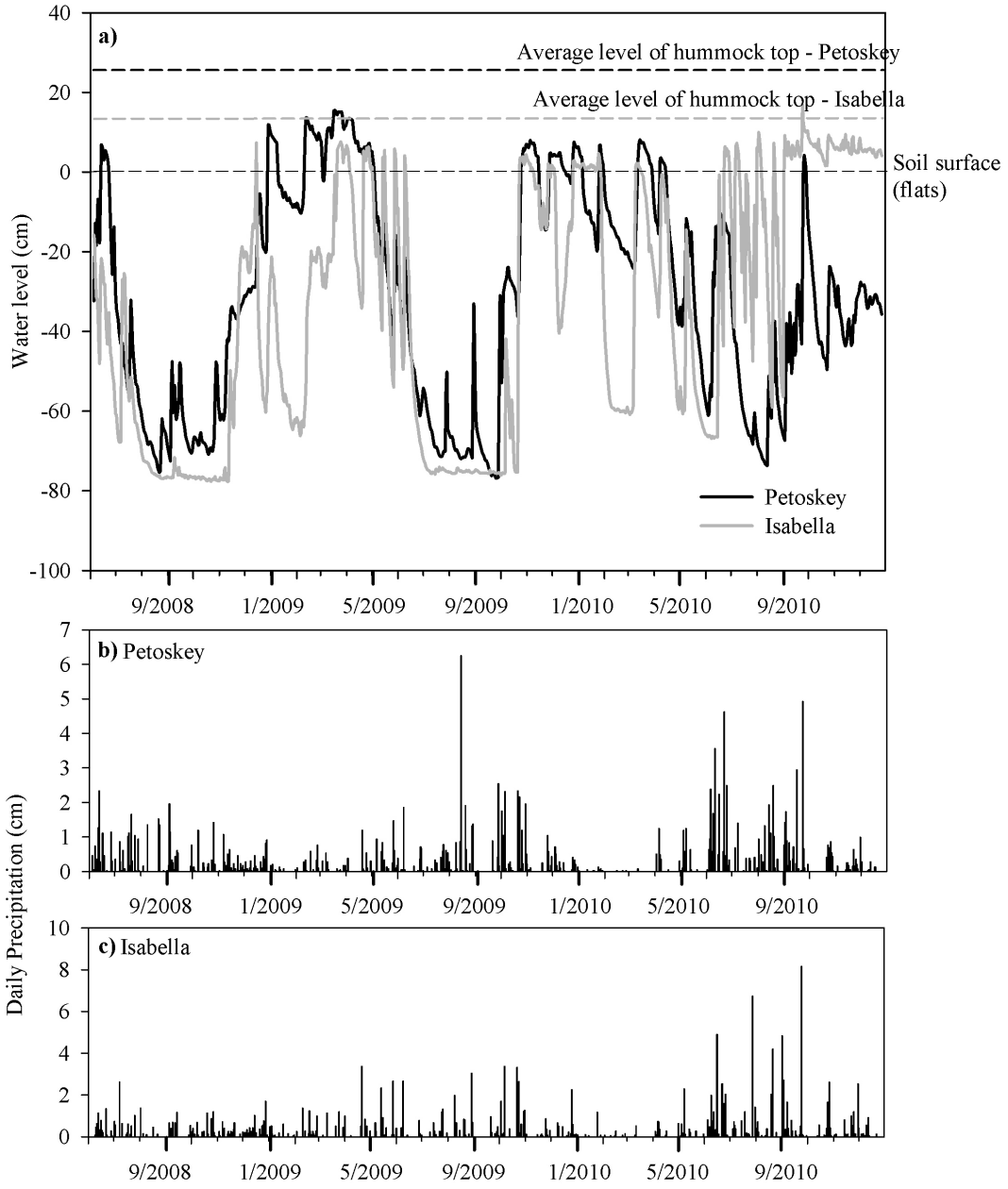

Figure 2.3 Mean water table levels for Isabella and Petoskey mitigation sites beginning one year after site creation (a) and daily precipitation for Petoskey (b) and Isabella (c). Water levels are the average of the three wells at each site. Horizontal dashed lines indicate ground surface level and average hummock heights at both sites (representing the elevation of planted flats and hummocks, respectively). Precipitation values are from nearest National Climatic Data Center (NOAA) gauging station to each study site (Pellston and Manistique, representing Petoskey and Isabella sites, respectively).

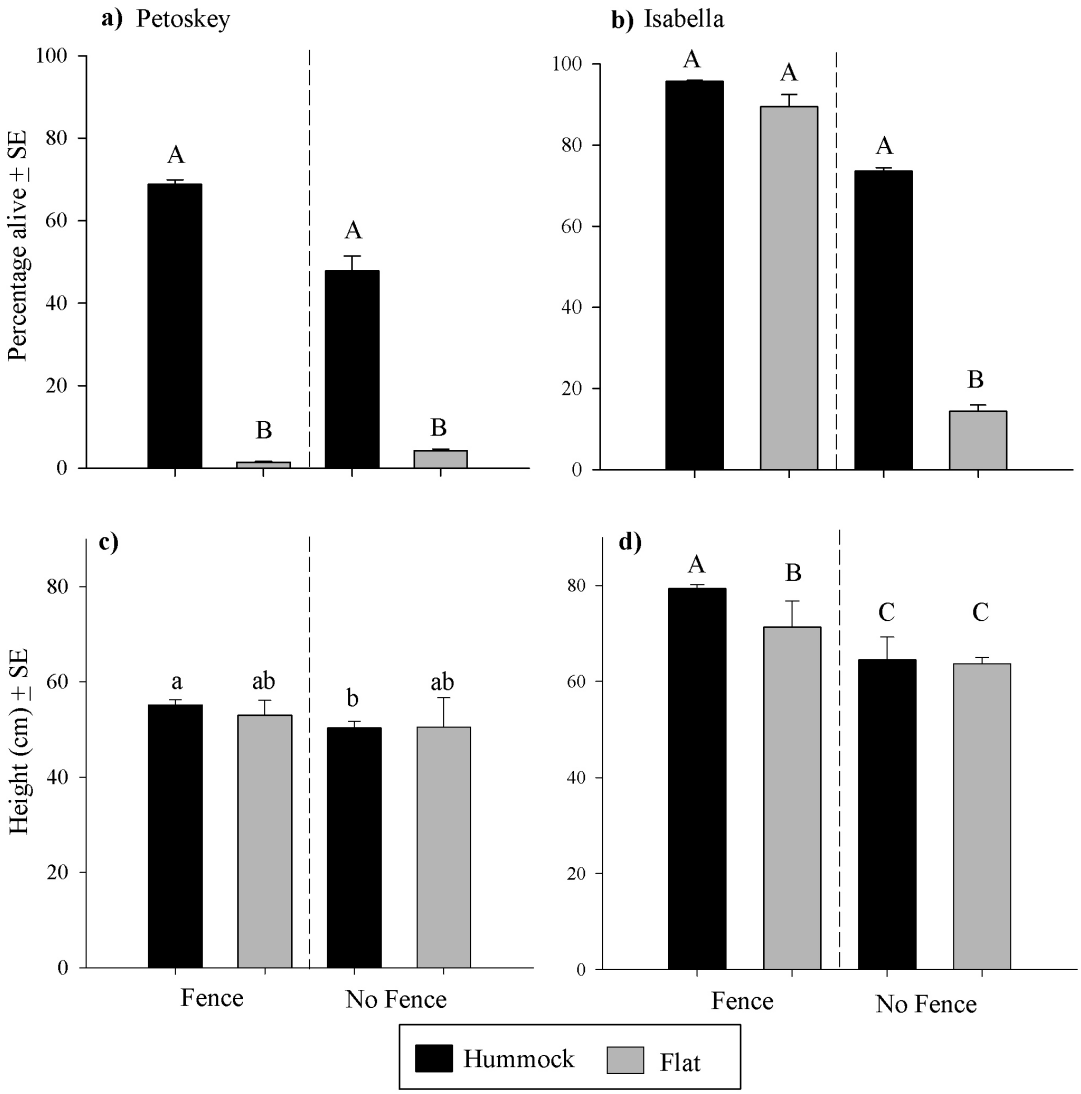

Figure 2.4 Northern white-cedar survival in Petoskey (a) and Isabella (b), and height of live trees in Petoskey (c) and Isabella (d) by microtopography and fencing. Bars on columns represent SE, and different lowercase and capital letters represent significant differences between means at $p < 0.10$ and $p < 0.05$, respectively (n = 6 for all treatment combinations except n =2 for Petoskey no fence flat; n = 2 for Isabella no fence hummock; n = 3 for Isabella fence flat).

Chapter 3: Changes in *Sphagnum* and feather moss ecophysiology along successional gradients in drained, restored, and pristine boreal spruce swamp forests[2]

3.1 Abstract

Boreal spruce swamp forests, in their natural state, harbor high biodiversity in the relatively species-poor northern landscape. They are also habitat for *Sphagnum* mosses, a keystone species for carbon accumulation. However, these wetlands have been extensively drained to improve conditions for forestry, which also results in a decline of *Sphagnum* and altered rates of carbon storage. Restoration has recently been taking place in spruce swamp forests. However, little is currently known about the effects of restoration on the physiological functioning of *Sphagnum*. The objective of this study was to evaluate the effects of land use change (drainage and restoration) on the ecophysiology of *Sphagnum* and feather mosses with regards to their carbon storage potential. We compared parameters of photosynthetic CO_2 exchange and chlorophyll fluorescence of the dominant *Sphagnum* and feather moss species across 3 restored, 3 drained, and 3 pristine spruce swamp forests in southern Finland monthly during the summer of 2011. Differences in ecophysiological parameters varied strongly by species. Feather mosses, in driest microhabitats, differed from *Sphagnum* species by having low dark respiration rates and positive photosynthetic C gain in low light. *S. riparium* occupied the wettest extreme of the water table gradient and had the highest photosynthetic capacity, net photosynthesis, and dark respiration. *S.riparium* dominated ditches of restored and drained sites; as a result, these land use types had higher photosynthetic productivity compared to pristine sites and drained and restored sites outside of the ditch line. Pristine and drained sites had similar ecophysiological response, although species type and cover strongly differed between the two land use types. Restored sites still differed from

[2] The content of this chapter includes material planned for journal submission.

pristine conditions based on species' ecophysiology 8–10 years after restoration; however, the higher productivity observed in restored sites will be important toward long-term peat development and carbon storage.

3.2 Introduction

Peatlands are wetlands that accumulate peat, and despite their relatively small land area, they store approximately one-third of world's soil carbon in the peat layer (Gorham 1991). In boreal peatlands, *Sphagnum* mosses form a dominant component of the ground cover and are key contributors to carbon storage through peat development (Gunnarsson 2005). However, the capacity of peatlands to sequester carbon can be altered following disturbances involved with land use change or long-term changes in climate (Gorham 1991).

Peatlands have been targeted for human use for centuries including uses such as peat harvesting for energy, farming, and forestry (Rydin and Jeglum 2006). Naturally, peatlands range from having an open canopy to a treed overstory, depending on site wetness. High water levels limit tree growth, and as a result, large areas of peatlands have been drained to stimulate tree production for forestry. To date, approximately 14 million ha in northern boreal regions worldwide have been drained (Paavilainen and Päivänen 1995). Nutrient-rich peatlands have been drained first and most extensively, notably boreal spruce mires, or spruce swamp forests (Hånell 1988). In some areas within northern Europe, for example in Finland, extensive drainage has led to the classification of these peatland types as threatened habitats (Eurola et al. 1991, Raunio et al. 2008) and some species typical to these ecosystems have been red-listed (Rassi et al. 2010).

Pristine spruce swamp forests are productive and diverse habitats (Ohlson 1997). In their pristine state, they support both a treed overstory and a *Sphagnum* mat in the shaded understory. The balance of these two components, however, becomes changed with drainage (Korpela 2004). Drier conditions favor tree growth but lead to a decrease in *Sphagnum* moss coverage. *Sphagnum* mosses tend to be replaced by bare soil or feather mosses (Laine et al. 1995), which have a lower ability to accumulate carbon (Turetsky et al. 2010).

Greater interest in recent years of how past land use has impacted peatlands has resulted in increasing efforts toward restoration, especially in conservation areas (Komulainen et al. 1999, Vasander et al. 2003). Restoration of peatlands drained for forestry involves damming or filling ditches with peat to elevate water tables to pre-restoration levels (Aapala and Tukia 2008). The goal of restoration usually includes creating conditions that permit the reestablishment of *Sphagnum* mosses and the ability to accumulate carbon (Robert et al. 1999; Waddington et al. 2003). Previous studies have shown that after rewetting forestry-drained peatlands, *Sphagnum* cover increases with a corresponding decrease in upland feather mosses (Komulainen et al. 1999, Jauhiainen et al. 2002, Aapala and Tukia 2008).

Research involving the restoration of forestry-drained peatlands has primarily focused on moss species composition through coverage estimates. Expanding beyond this, ecophysiological assessment at the species-level can be an indicator of overall ecosystem functioning. For example, photosynthesis rates obtained through measurements of CO_2 exchange (Granath et al. 2009) can provide insight regarding carbon accumulation. Measurements of chlorophyll fluorescence and quantum yield of PSII photochemistry can indicate plant stress due to water limitations, light intensity, and/or nutrient supply (Maxwell and Johnson 2000), allowing further exploration of the relationship between a species' physiology and the environment.

In this study, our objective was to to evaluate the effects of land use change (drainage and restoration) on the ecophysiology of *Sphagnum* and feather mosses regarding their carbon storage potential. As previous studies have revealed that photosynthetic responses of peatland mosses vary by season (i.e. Gaberščik and Martinčič 1987), this factor was taken into account to address our objective. We hypothesized that parameters of photosynthetic CO_2 exchange and chlorophyll fluorescence of *Sphagnum* and feather mosses will be affected by 1) time of year, 2) species, and 3) land use type. To address these hypotheses, we measured ecophysiological parameters throughout the growing season and for a diversity of species across the three land use types.

3.3 Materials and Methods

3.3.1 Study sites

Our study sites encompassed restored, drained, and pristine spruce swamp forests (n = 3 + 3 + 3) in southern Finland (Figure 3.1). Restored and drained sites had been drained by ditching for forestry to enhance tree growth. Currently drained sites were drained between 1908 and 1965 (Table 3.1); the date of drainage for restored sites is less certain, but between the period 1949 – 1980. Drainage had been successful, effectively increasing the volume of the tree stand in the sites. In 2001, one site (EV01VR) was restored by damming the drainage ditch (Table 3.1). In 2003, the remaining two sites were restored by filling the drainage ditches with peat. Restoration was conducted by the Finnish state forest agency (Metsähallitus). Restored and pristine sites are within state protected areas; all sites are governed by Metsähallitus.

Sites are located in the southern boreal zone with an average altitude of 150 m a.s.l. Climate conditions are boreal with a long-term mean annual temperature of 3.3 °C and annual precipitation that ranges from 680 to 713 mm depending on location.

All sites had an overstory with Norway spruce (*Picea abies*) as the dominant species, although volume differed by site (Table 3.1). The understory was dominated by *Vaccinium* dwarf shrubs. In pristine sites, *Sphagnum* mosses formed a nearly continuous mat on the forest floor. The sites lacked a strong hummock and hollow pattern, although decaying stumps and logs, as well as tree bases and roots, provided higher microhabitats where feather mosses were present. Cover of *Sphagnum* in drained sites was low, although greater coverage of *Sphagnum* could be found in and along the edges of drainage ditches. The cover of feather mosses, notably *Pleurozium schreberi* and *Hylocomnium splendens,* was greater in drained sites than pristine and restored sites. The restored sites had intermediate stages in moss cover between pristine and drained sites and differed depending on site water table. Sites are classified as *Vaccinium myrtillus* spruce mires (mustikkakorvet in Finnish) in the Finnish mire site type classification (Laine et al. 2012).

3.3.2 Sampling and sample preparation

Sampling took place monthly during the summer of 2011. Species selection aimed to capture the dominant moss species of each site, with three to four species selected per site (Table 3.1). *Pleurozium schreberi* and *Sphagnum girgensohnii*, which were common to all sites, were always collected regardless of dominance. In May during the first sampling, a total of four to six species per site were measured to assess the diversity in species response (Appendix B.1). Three replicates per species were collected. In restored and drained sites, *Sphagnum* was collected either from ditches or the remainder of the site ('main site') according to species (Figure 3.2): for the species measured in all months, *S. riparium* and *S. russowii* were always collected from the ditches (Appendix B.1). Samples were taken from their optimal habitat at each site and the top approx. 5 cm of stem was cut from a 25 cm^2 area. Mosses were placed in polyethylene bags to maintain moisture and after field collection were stored refrigerated at 5 °C in the dark.

At each moss collection point, peat moisture of the top 12 cm was measured using a CS-620 HydroSense (Campbell Scientific, Utah, USA) moisture meter. During each sampling period, site water table was measured manually from three perforated wells that transected the center of each site. In drained and restored sites, one well was located in the ditch line, and two wells transected the main site (Figure 2.2).

3.3.3 CO_2 exchange and chlorophyll fluorescence

To assess the potential of mosses as a carbon sink, we measured maximum net photosynthesis at high photosynthetic photon flux density (PPFD). Although 2000 µmol $m^{-2}s^{-1}$ has been used to replicate high light conditions in other studies, 1000 µmol $m^{-2}s^{-1}$ was chosen as the maximal light intensity that temporarily reaches the generally shaded understory of spruce swamp forests. Photosynthesis was also measured under differing light levels to assess productivity in shaded conditions. Parameters related to photosystem II (PSII) were measured to assess the acclimation of moss species to their habitats.

We conducted gas exchange and chlorophyll fluorescence measurements in the laboratory using a portable gas exchange fluorescence system GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany). We used a standard chamber of 4 × 2 cm, which was

modified to measure photosynthesis in spatial samples, such as moss shoot segments, in 1 cm high plexiglass cuvettes (frames) equipped with a mesh bottom surface to allow air to freely flow around the sample. We placed a uniform layer of *Sphagnum* capitula (corresponding to the top 10 mm) in the cuvette. The number of capitula used varied by species and ranged from 5 to 16. For feather mosses, the top 20 mm were cut and placed lengthwise in the cuvette, with stem numbers ranging from 4 to 11. Measurements were taken within two days of sample collection.

Prior to measurements, samples were removed from the dark and light-acclimated in the cuvettes for approx. 20 minutes under a PPFD of 1000 µmol $m^{-2}s^{-1}$ and ambient room temperature of approx. 22 °C. Net photosynthesis (A) was measured at decreasing levels of PPFD: 1000, 50, 25, and 0 µmol $m^{-2}s^{-1}$ (abbreviated as A_{1000}, A_{50}, A_{25}, and A_0) with artificial light provided by a built-in LED light source. Samples were allowed to acclimate to each light level prior to measurement until A was constant. During the measurement period, the chamber temperature was kept constant at 20 °C, the CO_2 concentration of incoming air was 400 ppm, air flow was 400 µmol s^{-1}, and relative humidity was maintained at approximately 90%.

Quantum yield of PSII photochemistry (Φ_{PSII}) was measured at the end of the 1000 µmol m^{-2} s^{-1} light level. Samples were then dark-acclimated for 6 – 12 hours at 5 °C, after which the ratio of variable and maximum fluorescence (F_v/F_m) was measured as the maximum quantum yield of PSII photochemistry, an indicator of stress response at PSII. After measurement, samples were dried to a constant weight, and A was expressed per unit dry mass (mg g^{-1} h^{-1}).

3.3.4 Data analysis

Photosynthetic activity was modeled using a nonlinear mixed-effects model. The model was based on the hyperbolic light saturation curve (i.e. Larcher 2003):

$$A_{ksi} = R_{ks} + \frac{PMAX_{ks}PPFD_{ksi}}{\alpha + PPFD_{ksi}} + e_{ksi} \quad (1)$$

where A_{ksi} is the observed net photosynthesis and $PPFD_{ksi}$ is the photosynthetic photon flux density for measurement i of sample s on site k. R_{ks} is measured dark respiration; $PMAX_{ks}$ is the photosynthetic capacity (the maximum rate of light-

saturated gross photosynthesis); and α is the maximum quantum yield of CO_2 assimilation calculated as the linear increase in A at low light levels. e_{ksi} is a normally distributed residual with mean zero and constant variance.

We assumed that parameters R_{ks} and $PMAX_{ks}$ are specific for each site and sample. However, parameter α was assumed to be constant over all samples and sites; this restriction was necessary because of the low number of observations per sample. The variation in respiration R_{ks} and maximum photosynthesis $PMAX_{ks}$ was explained by the fixed predictors moss species, land use type, month, water level, peat field moisture, and the sample dry weight. Sample dry weight was included in the analysis because a slight negative correlation (average R^2 by species = 0.26) was present between sample dry weight and A_{1000}, A_{50}, and A_{25} for most species and was found to improve the model fit. Dry weight was centered and standardized before being included in the model.

The final models for parameters R_{ks} and $PMAX_{ks}$, which are part of model 1, are defined below. All terms in the following models significantly explained the variation in response (approximate F- test, $p < 0.05$):

$$R_{ks} = SP_{ks} + MO_{ks} + L_{ks} + r_k + r_{ks} \quad (2)$$

$$PMAX_{ks} = SP_{ks} + MO_{ks} + L_{ks} + MC_{ks} + a_k + a_{ks} \quad (3)$$

where SP_{ks}, MO_{ks} and L_{ks} are factor-type predictors for species (9 levels), month (4 levels) and land use type (5 levels), respectively. MC_{ks} is the centralized dry mass of the sample having mean of zero. The last two terms in the equations are random effects for the site and sample, with bivariate normal distributions $(r_k, a_k)' \sim MVN(0, \Sigma_k)$ and $(r_{ks}, a_{ks})' \sim MVN(0, \Sigma_{ks})$. The model was fitted using using package nlme of the R software (Pinheiro and Bates 2000).

To determine differences in P_{max} and A_0 between species, land use type, and month, *post hoc* comparisons were made with the following contrasts: each land use type was compared against pristine; moss species were compared against *Sphagnum girgensohnii*; and months were compared against July. Pristine was chosen as the baseline land use type in order to determine how land use change has deviated from

natural conditions. Subsequently, *S. girgensohnii* was chosen because it is a common and characteristic moss species in pristine spruce swamp forests (Laine et al. 2009). July was chosen as the baseline month because it is commonly the period of peak growth in the study region (Riutta et al. 2007, Wilson et. al. 2007).

Linear mixed-effects models were used to determine the source of variation in light compensation point of A ($PPFD_c$), quantum yield of PSII photochemistry (Φ_{PSII}), and maximum quantum yield of PSII (F_v/F_m). Light compensation point of A was calculated as the x-intercept of the initial part of the A/PPFD curve (from A_0 to A_{50}). In the models, species, land use type, month, water table, and peat field moisture were included as fixed effects. Sample dry weight was included as a fixed effect in the model for $PPFD_c$ because it is derived from A_{50} and A_{25}. Site was included as a random effect, and $PPFD_c$, Φ_{PSII}, and F_v/F_m were each used as response variables. Fixed effects were eliminated from the model if found to be not significant. To determine differences in $PPFD_c$, Φ_{PSII}, and F_v/F_m between species, land use type, and month, *post hoc* comparisons were made using previously described contrasts. Models were fitted using package lme of the R software (Pinheiro and Bates 2000).

We used principal component analysis (PCA) to explore the main trends in the variation of photosynthetic response parameters (CO_2 assimilation rate at three levels of PPFD (A_{1000}, A_{25}, and A_0), light compensation point of A ($PPFD_c$), maximum quantum yield of PSII (F_v/F_m), and quantum yield of PSII (Φ_{PSII}) in relation to species, land use type, site water table, and peat field moisture. PCA was used due to the linear relationships between photosynthetic response variables. As patterns without seasonal variation would make them easier to interpret, only the May measurement period was used, as this month contained the greatest number of measured species.

Direct gradient analysis using redundancy analysis (RDA) was used to hierarchically partition the variation of photosynthetic response variables used in PCA. We conducted a series of (partial) RDA where the variance components higher in the hierarchy were taken as covariables. The hierarchical order of variance components is shown in Table 3.2. The order was focused to test our hypothesis with land use type as the main factor of interest. Only the species measured in all months were

included in the RDA analysis. This was done to avoid the bias in the impact of season as a result of the additional species measured in May. CANOCO for Windows 4.5 was used for analysis (ter Braak and Šmilauer 2002) and response variables were centered and standardized to make them comparable. In restored and drained sites, the ditch was considered a separate land use type in all analyses.

3.4 Results

Parameters of photosynthesis and chlorophyll fluorescence varied strongly between time of year, species, and land use type. The sum of measured environmental variables explained 68% of the variation in photosynthetic response parameters assessed in RDA (Table 3.2). Species differences explained the highest amount of variation (34%), followed by month (17%) and land use type (3.7%). Water table and peat field moisture each explained less than one percent of total variation.

3.4.1 Environmental conditions

The summer season 2011 (May – August) was warmer and drier than average summer conditions. The average summer temperature was 14.6 °C; 1.7 °C higher than the long-term average (1971–2000, Figure 3.3). Total summer precipitation was 230 mm, 49 mm less than the long-term average. Water table varied by land use type and month (Figure 3.4) and had a significant effect on variation in P_{max} ($p < 0.001$, Table 3.3), Φ_{PSII}, and F_v/F_m ($p < 0.01$, Table 3.4). Ditches of drained sites had the highest water table, followed by ditches in restored sites. Water levels of pristine sites were intermediate between restored and drained sites. The most similar water levels across land use type (excluding ditches) occurred in August (Figure 3.4). Peat field moisture varied within and across species.

3.4.2 CO_2 exchange

Photosynthetic capacity (P_{max}) and respiration (A_0) were significantly different across species, month, land use type, and water table ($p < 0.05$, Table 3.3). P_{max} for *S. girgensohnii* differed significantly from all other species except *Polytrichum commune* and *S. angustifolium* ($p < 0.05$, Table 3.5a). *Sphagnum riparium* had the highest P_{max}, A_0, and net photosynthesis (A_{1000}, Table 3.5a and Figure 3.5). P_{max} and

dark respiration were lowest for feather mosses *Pleurozium schreberi* and *Hylocomnium splendens*. P_{max} showed a slight increasing trend with increased peat field moisture, however, peat field moisture was better related to the distribution of species (Figure 3.6). Values for all measured photosynthetic parameters separated according to species, land use type, and month can be found in Appendix B, Tables B.2 to B.6, and Table B.7 includes species measured only in May.

P_{max} and A_0 were significantly higher in restored compared to pristine sites ($p < 0.05$ for restored ditches and $p < 0.1$ for restored, main site, Table 3.5b). P_{max} and A_0 were similar across pristine and drained (main site). P_{max} was lowest in May and varied little across summer months (June – August, Table 3.5c). Respiration was highest in May and June compared to July ($p < 0.05$ and $p < 0.1$, respectively) and August.

The effect of land use type and month on net photosynthesis rates differed according to species. A_{1000} was similar across land use type for *Pleurozium schreberi* and *S. magellanicum* (Figure 3.5a). *S. girgensohnii* and *S. riparium* had highest A_{1000} in restored sites, followed by the ditches of drained sites. Monthly variation in A_{1000} did not follow a consistent pattern across species, although generally an increasing trend in A_{1000} toward July was observed (Figure 3.7a).

Variation in light compensation point ($PPFD_c$) was significantly affected by species, land use type, and month ($p < 0.001$, Table 3.4). With the exception of *S. wulfianum*, $PPFD_c$ was highest in spring for all species followed by a sharp decline after which variation was less across the summer months (Figure 3.7c). $PPFD_c$ was lowest for the feather mosses (Table 3.6a and Figure 3.5c). *S. girgensohnii* had the lowest $PPFD_c$ across *Sphagnum* mosses.

3.4.3 Chlorophyll fluorescence

Absolute values for F_v/F_m varied between 0.59–0.82; average values by species ranged from 0.72–0.81 (Table 3.6 and Figure 3.5d). Low F_v/F_m values are associated with increased stress. Variation in F_v/F_m differed significantly across to species, month, land use type, water table level and peat field moisture ($p < 0.05$, Table 3.4). F_v/F_m was highest in August (Table 3.6c and Figure 3.7d), but did not differ significantly across land use type (Table 3.6b). Across species, F_v/F_m was highest for

S. girgensohnii, *S. wulfianum*, and *Polytrichum commune* and lowest for *S. riparium* and *S. magellanicum* (Table 3.6a).

Variation in quantum yield of PSII photochemistry (Φ_{PSII}) differed significantly across species, month, land use type, and water table level ($p < 0.05$, Table 3.4). Quantum yield of PSII photochemistry (Φ_{PSII}) for the feather mosses *H. splendens*, *P. commune*, and *P. schreberi* was on average about 50% higher than *Sphagnum* mosses (Table 3.6a and Figure 3.5e).

3.4.4 Relationships between photosynthetic response parameters

Principal components analysis indicated two strong gradients in the physiological response data (Figure 3.8). The main gradient covered 44% of variation of physiological parameters and can be described as a 'light-adaption' gradient similar to Hájek et al. (2009). This gradient separated *S. girgensohnii* from remaining *Sphagnum* species and feather mosses from all *Sphagnum* mosses. The second gradient was related to photosynthesis at high light (A_{1000}), the stress indicator F_v/F_m, and moisture (water table and peat field moisture). Described as an 'productivity and moisture' gradient, it explained 30% of the variation and separated individual *Sphagnum* species and land use types. Along this gradient, increased moisture corresponded to higher productivity and decreased stress.

3.5 Discussion

3.5.1 Comparison of parameters to previous studies

Photosynthetic capacity (P_{max}) in drained sites compared similarly to those by Hájek et al. (2009) in a forestry-drained minerotrophic peatland in southern Finland. However, values for net photosynthesis (A_{1000}) and P_{max} reported in this study were higher than those reported for *Sphagnum* and feather mosses in ombrotrophic bogs, permafrost forested peatlands, and oligotrophic fens (Skre and Oechel 1981, Granath et al. 2009 and 2010, Laine et al. 2011). Minerotrophic, shaded, and moist environments provide favorable growing conditions for *Sphagnum* mosses (Brock and Bregman 1989); these conditions are found in restored and pristine spruce swamp forests (Kuusinen 1996, Korpela 2004). In addition, the minerotrophic and dry

conditions of drained spruce swamp forests provide favorable conditions for the feather mosses (Laine et al. 1995). As a result, it follows that net photosynthesis rate would be greater for mosses in these habitats compared to other peatland types. Accordingly, greater biomass and height growth of *Sphagnum* mosses has been observed by Laiho et al. (2011) in drained minerotrophic peatlands compared to ombrotrophic sites.

F_v/F_m values were generally high compared to the value for unstressed plant and moss species, which is typically around 0.80 (Proctor 2010). These results indicate low levels of light-induced stress in comparison to other bryophyte data (Hájek et al. 2009, Laine et al. 2011, Zona et al. 2011). Due to the shade of the treed canopy, light-induced stress may only be a factor along the ditch line in restored sites where tree cover was less, which may be a cause for the drop in F_v/F_m in July for species measured in the ditch (*S. riparium* and *S. russowii,* Figure 3.7d).

3.5.2 Seasonal responses

Most previous work regarding *Sphagnum* seasonal growth pattern studies has been in ombrotrophic bogs, in which moss growth tends to be greatest in the spring and late summer or autumn (Silvola and Heikkinen 1979, Lindholm 1990, Laine et al. 2011). In contrast, we observed highest photosynthesis rates in mid-summer (July). Peatland type and its relationship to moisture availability is a critical driver for seasonal trends of moss growth in peatlands (Backéus 1988). This relationship has been observed by Laine et al. (2011), in which species from wet meadow and mesotrophic fen (wetter) habitats had greatest biomass production during summer, while biomass production of species in ombrotrophic bogs (drier habitats) was decreased during summer due to drought stress. Similarly, the shaded and relatively moist conditions of spruce swamp forests in this study provided suitable conditions for moss growth throughout the growing season. Although the water table was progressively lower during each sampling period (Figure 3.4), values of F_v/F_m increased toward August (Figure 3.7d). August was the driest month of the study, when mosses would be most prone to moisture limitations, but F_v/F_m revealed no obvious drought stress to photosystem II.

Seasonal trends of photosynthesis and respiration in this study compared more similarly to observations in black spruce/permafrost peatland in interior Alaska (Skre

and Oechel 1981). Skre and Oechel (1981) observed increasing rates of net photosynthesis to a maximum in August, as well as high dark respiration rates for all species in early spring. The gradual rise in photosynthesis has been interpreted by Skre and Oechel (1981) as increasing growth of young, photosynthetically active tissue over the course of the growing season. Acclimation of mosses to the increasing duration and intensity of light from spring to summer may have also been the cause of increasing monthly photosynthesis in this study, similarly to the short-term photosynthetic adaptions to changes in light conditions that has been observed in vascular plants (Larcher 2003). Skre and Oechel (1981) also interpreted the observed high spring respiration rates as a result of increased energy requirements for tissue repair and growth after frost damage. This may contribute to the high spring respiration in this study, as the dense tree canopy in spruce swamp forests results in slow warming, and snow can be found in spruce swamp forests even late into the spring season.

3.5.3 Land use type and moss strategies

Land use type had an important effect on the abundance and distribution of moss species (Maanavilja et al. unpublished) as well physiological differences across and within species. Changes in species composition and physiology are characteristics of successional change in both vascular plant and moss communities (Bazzaz 1979, Laine et al. 2011). Succession includes four key stages: disturbance, colonization, competitive interactions, and adjustment (MacMahon 1987). These elements are present in the disturbance (i.e. drainage or restoration) of spruce swamps, and changes in water level can be described as the primary disturbance. Principal components analysis indicated the spatial separation of land use type along the water table gradient (Figure 3.8). At the top of the gradient are drier, more stabilized sites (drained and pristine) with their commonly associated species (*S. magellanicum*, *S. russowii*, *S. angustifolium* and *P. schreberi*). At the lower end are wet and disturbed sites (restored sites and ditches) with their commonly associated species (*S. riparium* and *S. girgensohnii*), although *S. girgensohnii* is typical of pristine sites also.

Individual species had a strong effect on variation in physiological parameters, and the presence of multiple successional stages was likely a strong driver of the observed differences. Few species had the ecological amplitude to grow in all five land use

types in this study. Tolerance of most species to variable habitat types is lower, and most plants are adapted to specific habitats through their growth strategies. The three strategies, as defined by Grime (1977), can be placed along the successional gradient, with ruderal species occupying recently disturbed areas, competitive species during mid-succession, and stress-tolerant species at the adaption (late-successional) stage.

The late-successional stage of spruce swamp forests can be compared to forested vascular plant communities, where succession is associated with increased shade and decreased nutrient supply (Grime 1977). According to Bazzaz (1979), late-successional vascular species are highly efficient in low light and have low photosynthetic and dark respiration rates. For species that were present in multiple land use types in this study, A_{1000} and P_{max} were similar in the two late-successional stages (pristine and drained) and were lower than in restored sites and ditches (Figure 3.5a). F_v/F_m values in pristine sites were high for most species with the exception of *S. riparium*, indicating that the low observed A_{1000} and P_{max} were unlikely caused by stress to photosystem II. Low dark respiration rates were not consistently observed in pristine conditions, as considered characteristic of late-successional species. *S. wulfianum*, with lowest A_{1000} and P_{max} of all *Sphagnum* species, had a high rate of dark respiration. High dark respiration in late-successional stages may be caused by the metabolic costs of water conserving strategies, such as hummock formation and robust growth habit (Rice et al. 2008). The high respiration rate therefore resulted in a high light compensation point of some mosses in pristine conditions (Figure 3.5b and c).

In drained sites, the long time period since ditching (> 40 years) has resulted in communities acclimated to the prevailing dry and stable conditions. Feather mosses are well adapted to the low water levels and dense shade caused by drainage and increased tree volume (Laine et al. 1995, Fenton and Bergeron 2006). Feather mosses *Pleurozium schreberi* and *Hylocomium splendens*, in accordance with strategy of late-successional species, had low carbon assimilation and dark respiration rates and low light compensation points in drained habitats (Figure 3.5). The drained conditions were poor, however, for *Sphagnum* productivity. *S. magellanicum* and *S. angustifolium* were among the species that managed to persist. They formed tight cushions with limited surface roughness to maximize water retention and minimize

water loss through evaporation (Clymo 1973). A_{1000} for both species was similar between drained and pristine conditions; however, lower F_v/F_m indicated stress to photosystem II as a possible result of dessication. The ditches of drained sites offered a more suitable refuge for *Sphagnum* species to persist, most commonly *S. riparium*. In spring, water level was high enough in these ditches to allow *Sphagnum* mosses to have similar high A_{1000} to the ditches in restored sites.

Following restoration, higher water levels enable *Sphagnum* cover to expand from remnant patches that persisted throughout drainage, while the cover of feather mosses decreases and becomes restricted to the driest microhabitats (Jauhiainen et al. 2002). Following the disturbance of rewetting and subsequent colonization, restored sites and the species in them are now in the competitive stage (Grime 1977, MacMahon 1987**)**. Successful mosses in this stage will be able to outcompete competitors through fast and efficient utilization of resources such as nutrients, light, and space (Grime 1977). *S. girgensohnii* is a successful competitor in these conditions, as it is the dominant moss species in restored sites (Maanavilja et al. unpublished), and has the highest A_{1000} of all species in restored sites outside the ditch line. Previous research indicates *S. girgensohnii* to be an opportunist species in new habitat and has been shown to be a key driver of paludification of spruce forests (*Picea sitchensis*) in North America (Noble et al. 1984). Disturbances to the forest floor, together with increased water table, both contribute to the increasing dominance of *S. girgensohnii* in those forests. Indicators of stress response from this study indicate a fairly large ecological amplitude for the species, as values of F_v/F_m were always high, except for a slight decline in drained sites. *S. girgensohnii* also differed from remaining *Sphagnum* mosses by its lower light compensation point, indicating suitability to the shaded habitat of spruce swamp forests.

Ditches of restored sites are still distinguished from the remainder of the spruce swamp 8 to 10 years after restoration. Ditches are sites of highly productive *Sphagnum* cover, primarily *S. riparium*. *S. riparium* is most commonly found at the surface water level (Gignac et al. 1991), and is frequently a pioneering species in rewetted peatlands (Zoltai 1993). *S. riparium* displayed characteristics of ruderal vascular plants (Grime 1977, Laine et al. 2011), with high A_{1000}, P_{max}, and dark respiration. During succession, competitive species replace ruderals as environmental

conditions change (Grime 1977). Over time, the high rate of production of *S. riparium* will accelerate terrestrialization of the ditch line, which will lower the relative water table and create suitable microhabitat for other species. Already in some restored sites, species such as *S.russowii* and *S.girgensohnii* have been invading the ditch line in the drier microhabitats.

3.5.4 Ecological Implications

An objective of this study was to determine how drainage and restoration affect the richness of species' functional types in the moss layer, and the implications of restoration for carbon accumulation. The ruderal species *S. riparium* is an important component of restored sites. With its high rate of carbon assimilation, it is able to quickly accumulate biomass (Maanavilja et al. unpublished) and has an important effect toward accumulation of stored carbon. Other ruderal species such as *Sphagnum fimbriatum* (Laine et al. 2011) and *S. squarrosum* may perform similar functions in restored sites. While ruderal species may be outcompeted by other species of *Sphagnum* as sites become drier, they have an important role in the initial stages following restoration.

Competitive species play a key role in utilizing rewetted habitat throughout the restored area. While A_{1000} and P_{max} were lower for competitors than ruderal species, photosynthetic rates were still higher in restored than pristine and drained sites. These competitive species are important to more wide-spread carbon accumulation outside the ditch line. *S. girgensohnii* was the key competitor identified in this study for spruce swamp forests, which had the highest $A_{1000,}$ $P_{max,}$ and F_v/F_m in restored sites.

S. girgensohnii, together with *S. russowii*, was also an important component of the *Sphagnum* community in pristine spruce swamp forests, thus, its contribution toward carbon accumulation will continue even in the later successional stages. However, as water levels decrease due to increased peat development in restored sites, species that can acclimate to drier conditions are also important for succession toward pristine conditions. Species such as *S. magellanicum*, *S. angustifolium*, and *S. wulfianum* will be important to carbon accumulation in drier microhabitats, as well as when restoration results in drier conditions than desired.

The contributions of ruderal and competitive species resulted in higher A_{1000} and P_{max} in restored sites than pristine or drained sites (Table 3.5 and Figure 3.5a). However, in contrast with expectations, when compared at the treatment level, all physiological parameters were similar between pristine and drained sites above the ditch (Table 3.5 and Table 3.6). Determining ecosystem function must take into account not only measurements of physiological parameters from individual species, but a consideration of species' functional type regarding habitat preference and decomposition as well as total abundance of the measured species in order to apply results to the ecosystem level. *Sphagnum* has been shown to be a more important contributor to carbon storage than feather mosses, as its tissues decompose slower (Turetsky et al. 2010), and it more commonly occupies wet, anoxic environments that further slow decomposition (Rydin and Jeglum 2006). *Sphagnum* cover, as well as total moss cover, was less in drained sites than pristine (Table 3.1, Maanavilja et al. unpublished). While *Sphagnum* formed an extensive mat on the forest floor in pristine conditions, mosses were isolated to small patches in drained sites. Application of carbon assimilation values to moss area would therefore result in greater carbon assimilation in pristine sites.

Conclusions

Land use type had only a small direct effect on physiological response of mosses in spruce swamp forests. Therefore, we propose that the successional changes that occur with drainage, rewetting, and development of pristine conditions have a direct effect on species composition and physiogical response (Figure 3.9). In the short term (8–10 years after rewetting), restoration favors different growth strategies than in pristine conditions. Ruderal and competitive species, identified here by high rates of photosynthetic capacity and net photosynthesis, are more productive than late-successional species and can lead to greater carbon accumulation during the initial stages following rewetting.

Evaluation of restoration success regarding *Sphagnum* productivity has commonly been done using biomass and cover estimates; however, biomass sampling is time and labor intensive. Measurements of ecophysiological response can be done during one sampling period and yield immediate results. Assessment of photosynthetic parameters in this study were comparable to trends of productivity through biomass

estimates (Maanavilja et al. unpublished). Therefore, a combination of moss ground cover estimates and ecophysiological assessment of the dominant species could be an effective method to evaluate restoration success and successional stages. In this study, net photosynthesis had the strongest differences across species during the measurement periods in late June and late July, making mid-summer the recommended time period for a one-time sampling of ecophysiological parameters in spruce swamp forests.

Tables

Table 3.1

Locations and characteristics of study sites (P. schr. = P. schreberi, S. girg. = S. girgensohnii, S. mage. = S. magellanicum, S. ripa. = S. riparium, S. russ. = S. russowii, S. wulf. = S. wulfianum).

Site	Northing, Easting	Status	pH (se)[1]	Year of restoration (drainage)	*Sphagnum* cover (%)[1]	Feather moss cover (%)[1]	Sampled moss species[2]		Dominant vascular species[1]	Tree stand volume (m^3)	Average water table depth (cm)[3]	Average peat depth, cm (se)[1]
EvLuVK	61°14'34" 25°03'22"	Pristine	4.09 (0.05)	-	47	9	*P. schr.* *S. girg.*	*S. mage.* *S. wulf.*	*Vaccinium myrtillus* *Vaccinium vitis-idaea* *Dryopteris carthusiana*	280	–30	>145
SusiLu	61°51'31" 24°14'07"	Pristine	4.12 (0.12)	-	69	6	*P. schr.* *S. girg.*	*S. ripa.* *S. russ.*	*Vaccinium vitis-idaea* *Vaccinium myrtillus* *Eriophorum vaginatum*	259	–16	89 (8.3)
EvLuPa	61°15'07" 25°03'45"	Pristine	4.02 (0.04)	-	56	8	*P. schr.* *S. girg.* *S. mage.*		*Vaccinium myrtillus* *Vaccinium vitis-idaea* *Rubus chamaemorus*	217	–34	>132
Ev03ku	61°13'18" 25°04'05"	Restored (via ditch filling)	3.88 (0.08)	2003	8	25	*P. schr.* *S. girg.* *S. ripa.*		*Vaccinium myrtillus* *Vaccinium vitis-idaea* *Dryopteris carthusiana*	287	–34	>145
Ev03ma	61°12'52" 25°03'32"	Restored (via ditch filling)	4.09 (0.03)	2003	33	11	*P. schr.* *S. girg.*	*S. ripa.* *S. russ.*	*Vaccinium vitis-idaea* *Vaccinium myrtillus* *Lycopodium annotinum*	275	–14	>132
Ev01VR	61°13'51" 25°04'27"	Restored (via ditch blocking)	4.06 (0.07)	2001	25	21	*P. schr.* *S. girg.* *S. ripa.*		*Vaccinium myrtillus* *Dryopteris carthusiana* *Carex globosa*	181	–13	>145
LakkOj	61°47'57" 24°18'07"	Drained	4.44 (0.14)	(1949)	5	13	*P. schr.* *S. girg.*	*S. mage.*	*Vaccinium myrtillus* *Vaccinium vitis-idaea*	334	–25	115 (4.7)
KoniOj	61°47'44" 24°17'43"	Drained	4.02 (0.03)	(1965)	19	21	*P. schr.* *S. girg.* *S. mage.*		*Vaccinium uliginosum* *Athyrium filix-femina* *Eriophorum vaginatum*	298	–43	114 (13.3)
VesiOj	61°22'43" 25°06'37"	Drained	4.09 (0.04)	(1908-1913)	3	18	*P. schr.* *S. girg.* *S. ripa.*		*Vaccinium myrtillus* *Vaccinium vitis-idaea* *Oxalis acetosella*	319	–63	>145

1. Maanavilja et al. unpublished
2. Species sampled June – August.
3. Average across the 4 sampling periods.

Table 3.2
Hierarchical partitioning of physiological response parameters (CO_2 assimilation rate at three levels of PPFD (A_{1000}, A_{25}, and A_0), light compensation point of A ($PPFD_c$), maximum quantum yield of PSII (F_v/F_m), and quantum yield of PSII (Φ_{PSII})) based on a series of redundancy analyses. In each analysis the variables above were taken as covariables. Interaction terms were not used as covariables.

Source of variation	Amount of variation explained (%)	*F*-value	*P*-value
Month	17.2	24.7	0.002
Species	34.3	49.5	0.002
Land use type	3.7	7.2	0.002
Land use type × Species	1.4	1.8	0.008
Land use type × Month	5.4	3.8	0.002
Month × Species	5.0	2.8	0.002
Site water table	0.6	4.3	0.006
Peat field moisture	0.4	2.8	0.056
Total	68.0		

Table 3.3
ANOVA results from non-linear mixed effects model of the light response curve.

Source	num DF	den DF	F-value	p-value
α	1	1202	4764.81	<.001
P_{max} (Intercept)	1	1202	531.335	<.001
P_{max} (Species)	8	1202	32.652	<.001
P_{max} (Month)	3	1202	53.561	<.001
P_{max} (Water table level)	1	1202	16.565	0.001
P_{max} (Land use type)	4	1202	2.812	0.024
P_{max} (Sample dry weight)	1	1202	170.035	<.001
A_0 (Intercept)	1	1202	805.264	<.001
A_0 (Species)	8	1202	93.266	<.001
A_0 (Month)	3	1202	36.949	<.001
A_0 (Land use type)	4	1202	2.82	0.024

Table 3.4
ANOVA results from linear mixed-effects model for light compensation point ($PPFD_c$), maximum quantum yield of PSII (F_v/F_m), and quantum yield of PSII (Φ_{PSII}).

	$PPFD_c$ (μmol $m^{-2}s^{-1}$)				Φ_{PSII}				F_v/F_m			
Source	num. df	den. df	F-value	p-value	num. df	den. df	F-value	p-value	num. df	den. df	F-value	p-value
Intercept	1	387	1330.9	<.001	1	397	11058.5	<.001	1	387	50156.8	<.001
Species	8	387	68.7	<.001	8	397	54.9	<.001	8	387	12.8	<.001
Month	3	387	69.8	<.001	3	397	41.3	<.001	3	387	70.0	<.001
Land use type	4	387	5.6	<.001	4	397	12.8	<.001	4	387	5.7	<.001
Water table level					1	397	13.5	<.001	1	387	8.0	0.005
Peat field moisture									1	387	5.8	0.017
Sample dry weight	1	387	46.1	<.001								

Table 3.5

Post hoc contrast results from the non-linear mixed effects model: maximum photosynthetic rate (P_{max}) and dark respiration (A_0) from the light response model according to species (a), land use type (b), and month (c). P-values indicate significant differences from *S. girgensohnii*, pristine, and July, respectively. Means ± SE.

(a) Species	*n*	P_{max} (mg g^{-1} h^{-1})	p-value	A_0 (mg g^{-1} h^{-1})	p-value
Hylocomium splendens	2	4.45 ± 0.25	**<0.001**	–0.63 ± 0.03	**<0.001**
Pleurozium schreberi	36	4.45 ± 0.1	**<0.001**	–0.43 ± 0.02	**<0.001**
Polytrichum commune	1	8.65 ± 0.91	0.104	–1.43 ± 0.1	0.554
S. angustifolium	7	5.59 ± 0.37	0.996	–1.66 ± 0.04	**0.032**
S. girgensohnii	36	6.86 ± 0.15	-	–1.12 ± 0.02	-
S. magellanicum	18	5.36 ± 0.17	**<0.001**	–1.11 ± 0.03	0.851
S. riparium	20	8.91 ± 0.28	**<0.001**	–1.99 ± 0.04	**<0.001**
S. russowii	12	5.73 ± 0.34	**<0.001**	–1.36 ± 0.04	0.531
S. wulfianum	6	4.94 ± 0.29	**0.004**	–1.39 ± 0.09	0.095

(b) Land use type	*n*	P_{max} (mg g^{-1} h^{-1})	p-value	A_0 (mg g^{-1} h^{-1})	p-value
Drained, ditch	6	8.06 ± 0.55	0.118	–1.61 ± 0.07	0.861
Drained, main site	35	5.26 ± 0.15	0.825	–0.90 ± 0.04	0.176
Pristine	49	5.35 ± 0.13	-	–0.97 ± 0.04	-
Restored, ditch	19	8.69 ± 0.29	**0.016**	–1.80 ± 0.07	**0.007**
Restored, main site	29	6.09 ± 0.21	0.087	–1.08 ± 0.06	**0.008**

(c) Month	*n*	P_{max} (mg g^{-1} h^{-1})	p-value	A_0 (mg g^{-1} h^{-1})	p-value
May	48	5.68 ± 0.17	**0.035**	–1.42 ± 0.04	**<0.001**
June	30	6.47 ± 0.26	0.785	–1.02 ± 0.06	**0.077**
July	30	6.4 ± 0.25	-	–0.92 ± 0.06	-
August	30	5.93 ± 0.17	0.147	–0.92 ± 0.06	0.963

Table 3.6

Post hoc contrast results from the linear-mixed effects model: light compensation point ($PPFD_c$), maximum quantum yield of PSII (F_v/F_m), and quantum yield of PSII (Φ_{PSII}) according to species (a), land use type (b), and month (c). P-values indicate significant differences from *S. girgensohnii*, pristine, and July, respectively. Means ± SE.

(a) Species	*n*	$PPFD_c$ (μmol $m^{-2}s^{-1}$)	p-value	F_v/F_m	p-value	Φ_{PSII}	p-value
Hylocomium splendens	2	17.1 ± 1.77	**0.022**	0.72 ± 0.006	0.724	0.18 ± 0.01	**0.001**
Pleurozium schreberi	36	13.7 ± 0.56	0.998	0.74 ± 0.003	**0.001**	0.18 ± 0.005	**<0.001**
Polytrichum commune	1	17.8 ± 0.44	0.361	0.81 ± 0.01	**<0.001**	0.18 ± 0.012	**0.023**
S. angustifolium	7	34 ± 1.21	**0.009**	0.73 ± 0.008	0.104	0.13 ± 0.006	**0.01**
S. girgensohnii	36	18.7 ± 0.6	-	0.76 ± 0.003	-	0.1 ± 0.002	-
S. magellanicum	18	24.4 ± 1.34	**<0.001**	0.73 ± 0.006	**<0.001**	0.09 ± 0.003	0.275
S. riparium	20	27.3 ± 1.18	**<0.001**	0.74 ± 0.005	**<0.001**	0.1 ± 0.004	0.353
S. russowii	12	28.9 ± 1.75	**<0.001**	0.75 ± 0.007	0.481	0.12 ± 0.005	**0.006**
S. wulfianum	6	29.2 ± 1.84	0.684	0.77 ± 0.005	0.111	0.13 ± 0.005	**<0.001**

(b) Land use type	*n*	$PPFD_c$ (μmol $m^{-2}s^{-1}$)	p-value	F_v/F_m	p-value	Φ_{PSII}	p-value
Drained, ditch	6	24.1 ± 2.47	**0.034**	0.75 ± 0.007	0.772	0.09 ± 0.005	**<0.001**
Drained, main site	35	20.7 ± 0.94	**0.035**	0.73 ± 0.004	0.169	0.12 ± 0.005	0.596
Pristine	49	21.1 ± 0.83	-	0.75 ± 0.003	-	0.12 ± 0.004	-
Restored, ditch	19	24.5 ± 1.19	0.655	0.76 ± 0.005	0.428	0.11 ± 0.004	0.838
Restored, main site	29	20.5 ± 1.06	0.096	0.76 ± 0.004	0.471	0.15 ± 0.006	0.145

(c) Month	*n*	$PPFD_c$ (μmol $m^{-2}s^{-1}$)	p-value	F_v/F_m	p-value	Φ_{PSII}	p-value
May	48	28.9 ± 0.79	**<0.001**	0.73 ± 0.003	**<0.001**	0.14 ± 0.004	**<0.001**
June	30	17.8 ± 0.77	**0.04**	0.76 ± 0.002	**0.0003**	0.12 ± 0.006	0.194
July	30	16.7 ± 0.81	-	0.74 ± 0.004	-	0.1 ± 0.004	-
August	30	18.1 ± 0.78	0.218	0.78 ± 0.002	**<0.001**	0.13 ± 0.005	**<0.001**

Figures

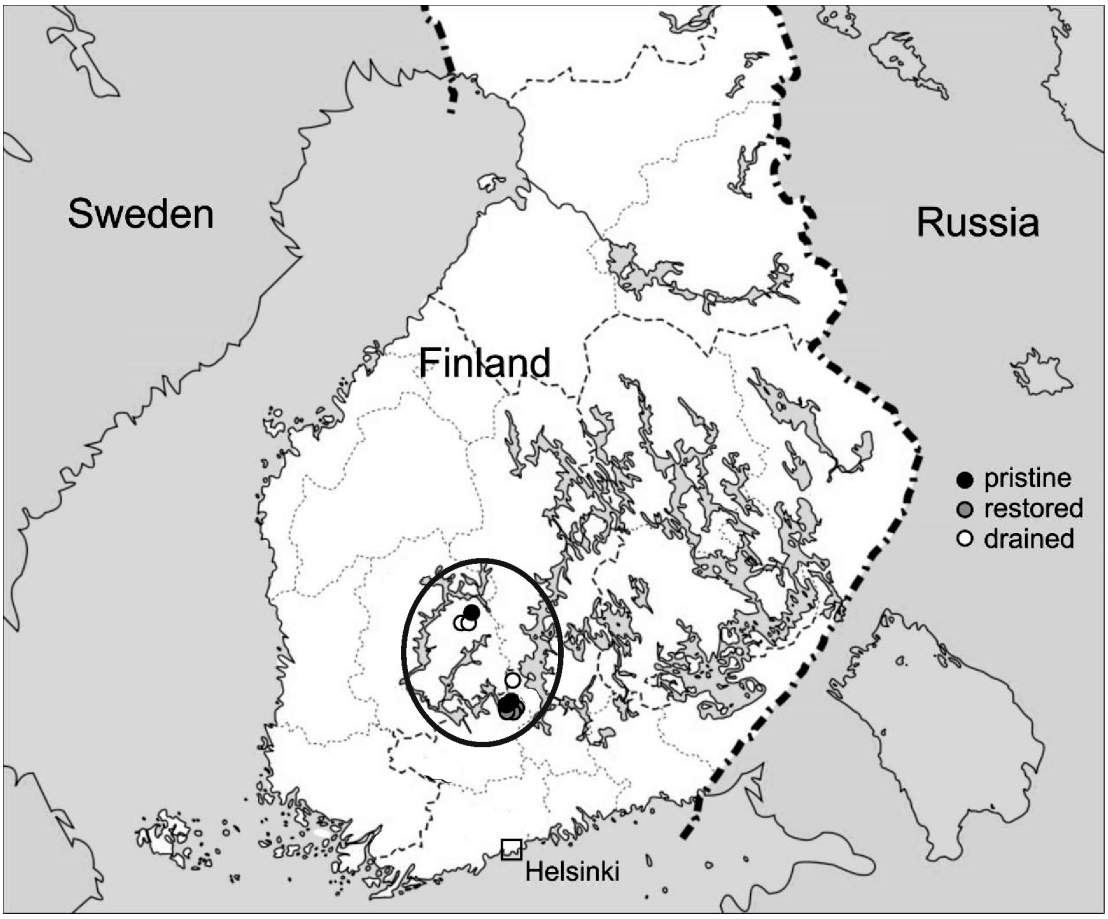

Figure 3.1 Location of the study sites.

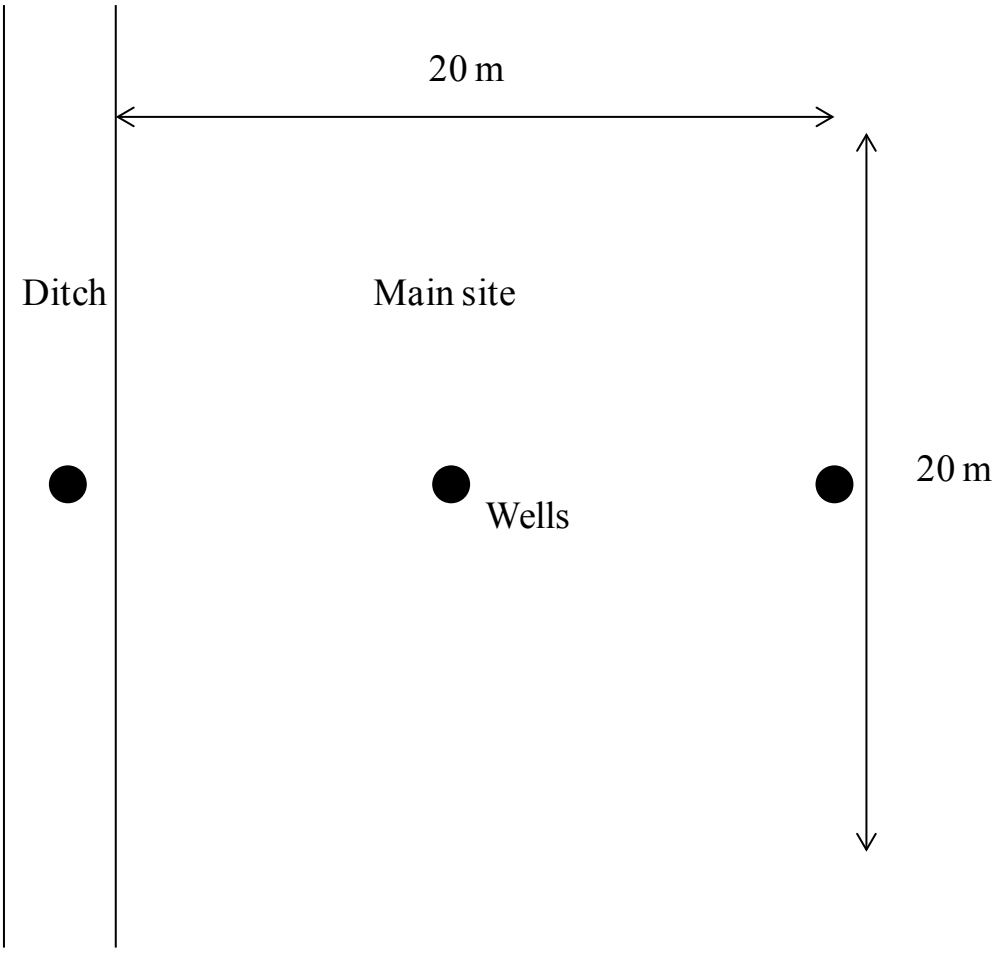

Figure 3.2 Diagram of restored and drained study sites.

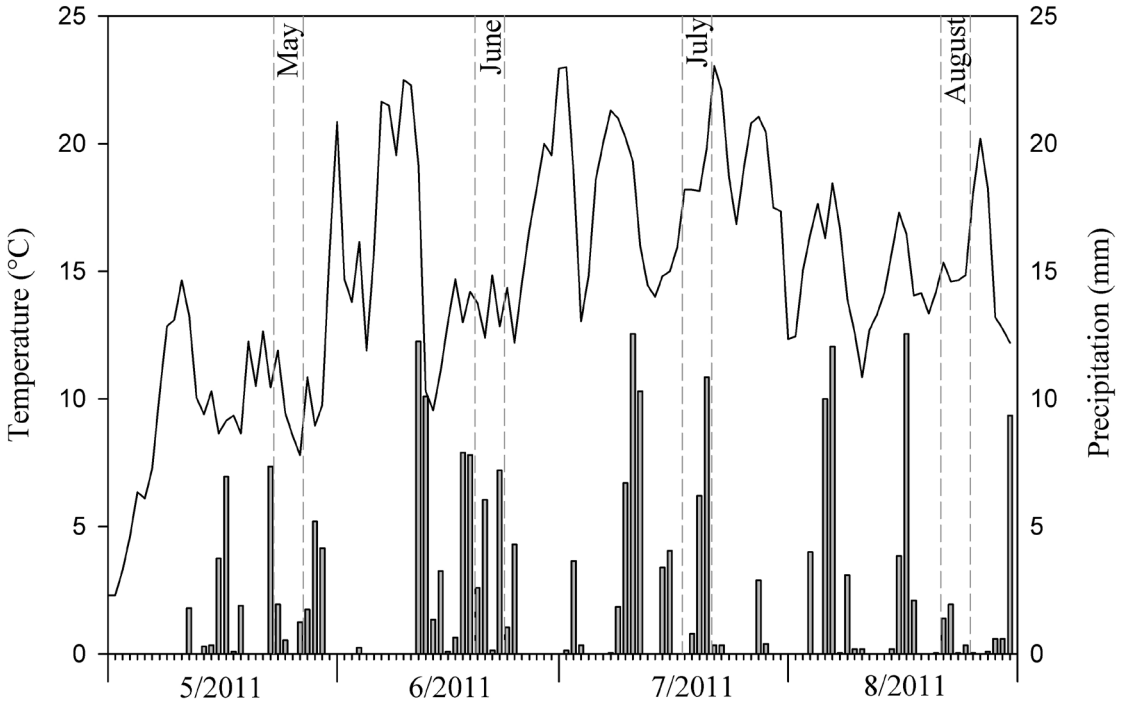

Figure 3.3 Daily temperature (line graph) and precipitation (bar chart) data for the study sites. Monthly sampling periods are outlined by dashed vertical lines. Temperature and precipitation data are averages from the nearest weather stations to the study areas (Hämeenlinna Lammi Evo and Juupajoki Hyytiälä weather stations).

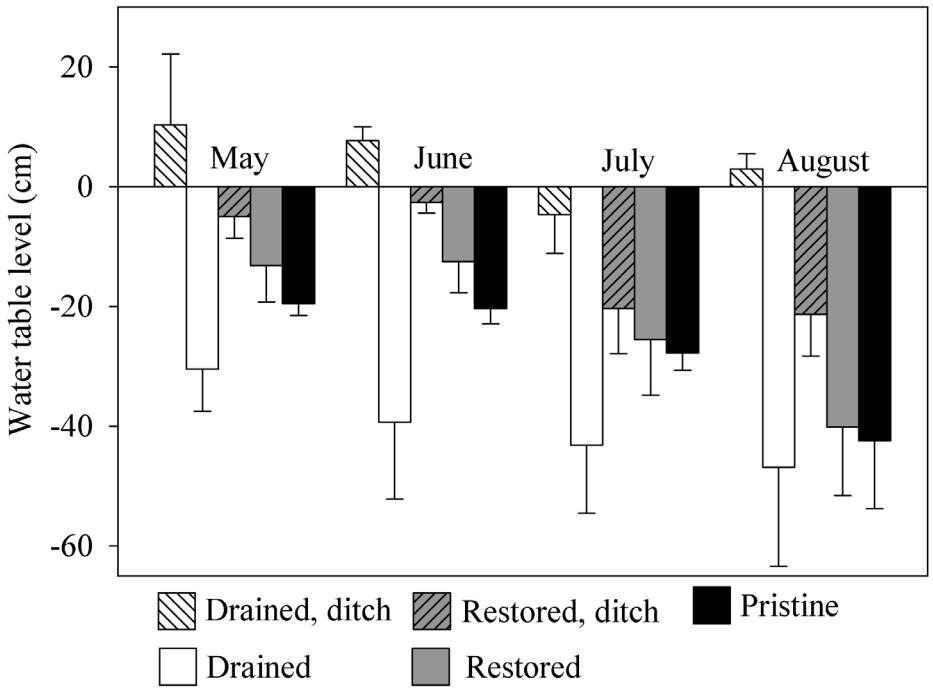

Figure 3.4 Average water table level by land use type and month.

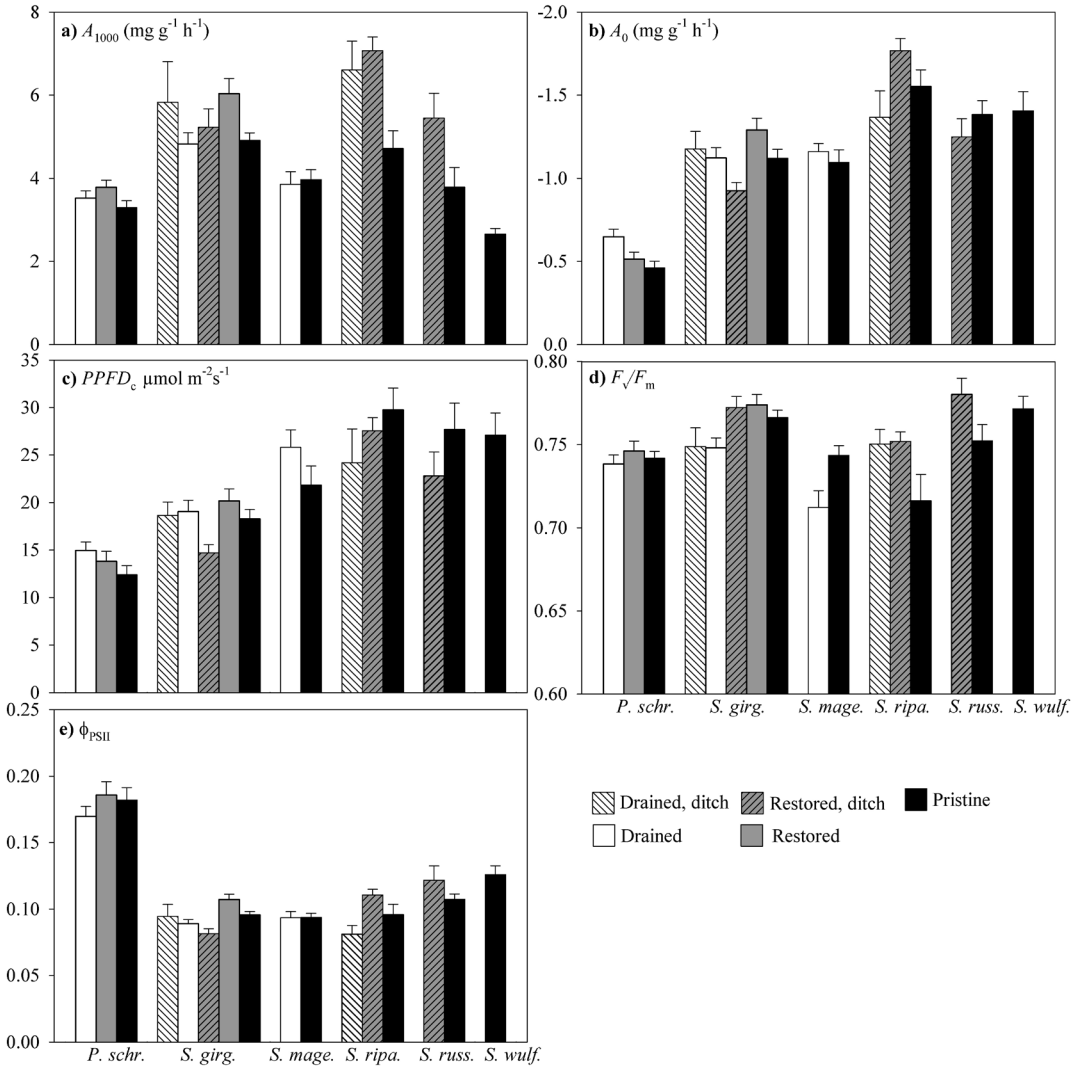

Figure 3.5 Variation in photosynthetic response and chlorophyll fluorescence parameters by species and land use type. Includes data only for species measured during all four measurement periods. Bars on columns indicate SE (*P. schr. = P. schreberi, S. girg. = S. girgensohnii, S. mage. = S. magellanicum, S. ripa. = S. riparium, S. russ. = S. russowii, S. wulf. = S. wulfianum*).

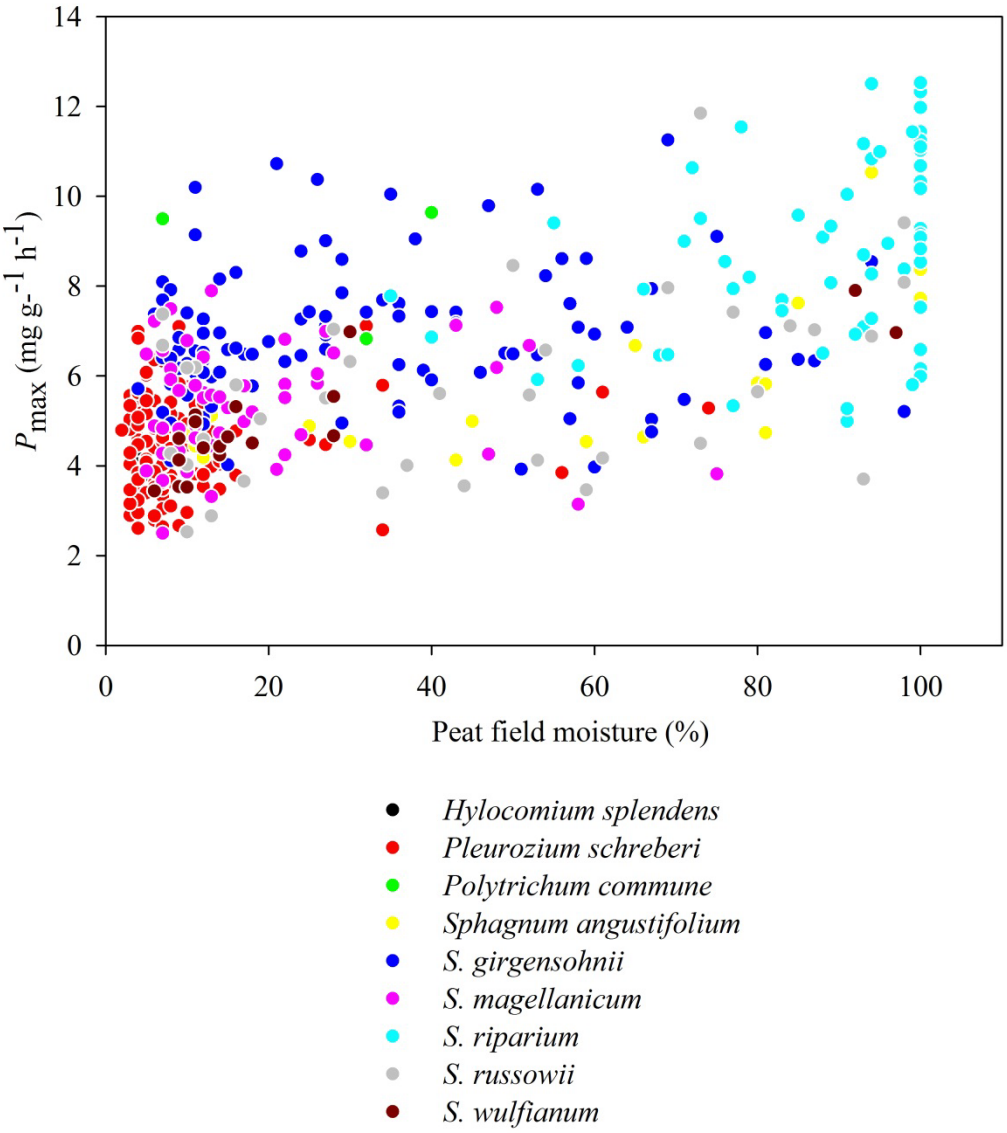

Figure 3.6 Maximum photosynthesis (P_{max}) versus peat field moisture according to species.

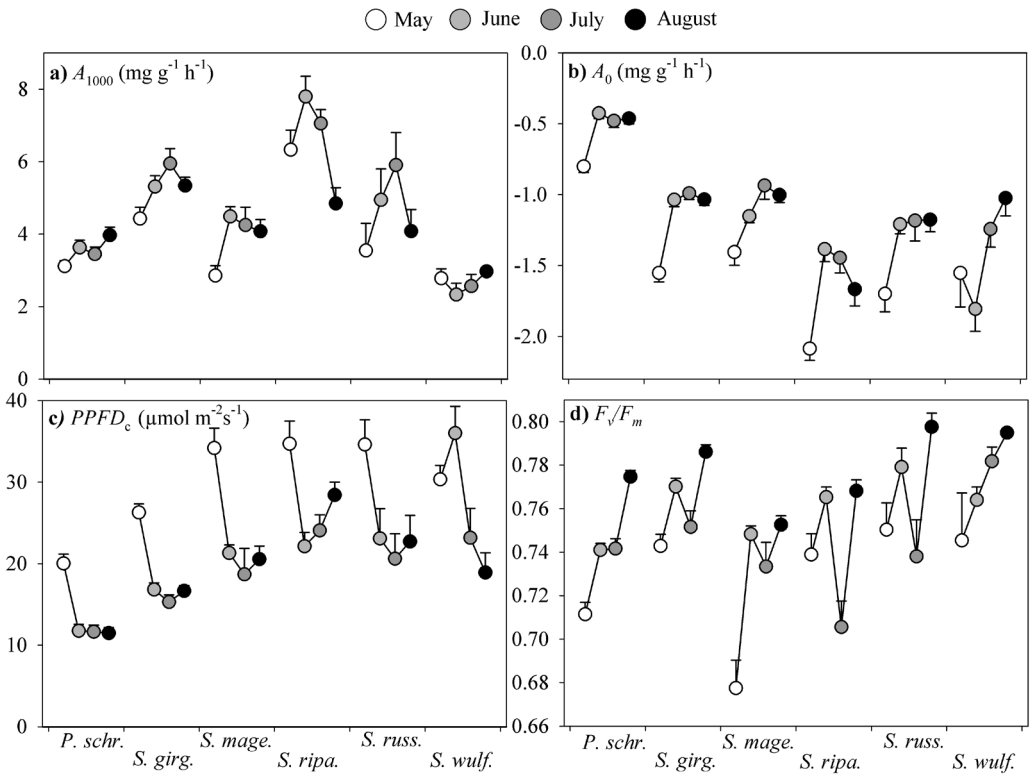

Figure 3.7 Variation in photosynthetic response and chlorophyll fluorescence parameters by species and month. Includes data only for species measured during all four measurement periods. Bars indicate SE (*P. schr = P. schreberi, S. girg. = S. girgensohnii, S. mage. = S. magellanicum, S. ripa = S. riparium, S. russ. = S. russowii, S. wulf = S. wulfianum*).

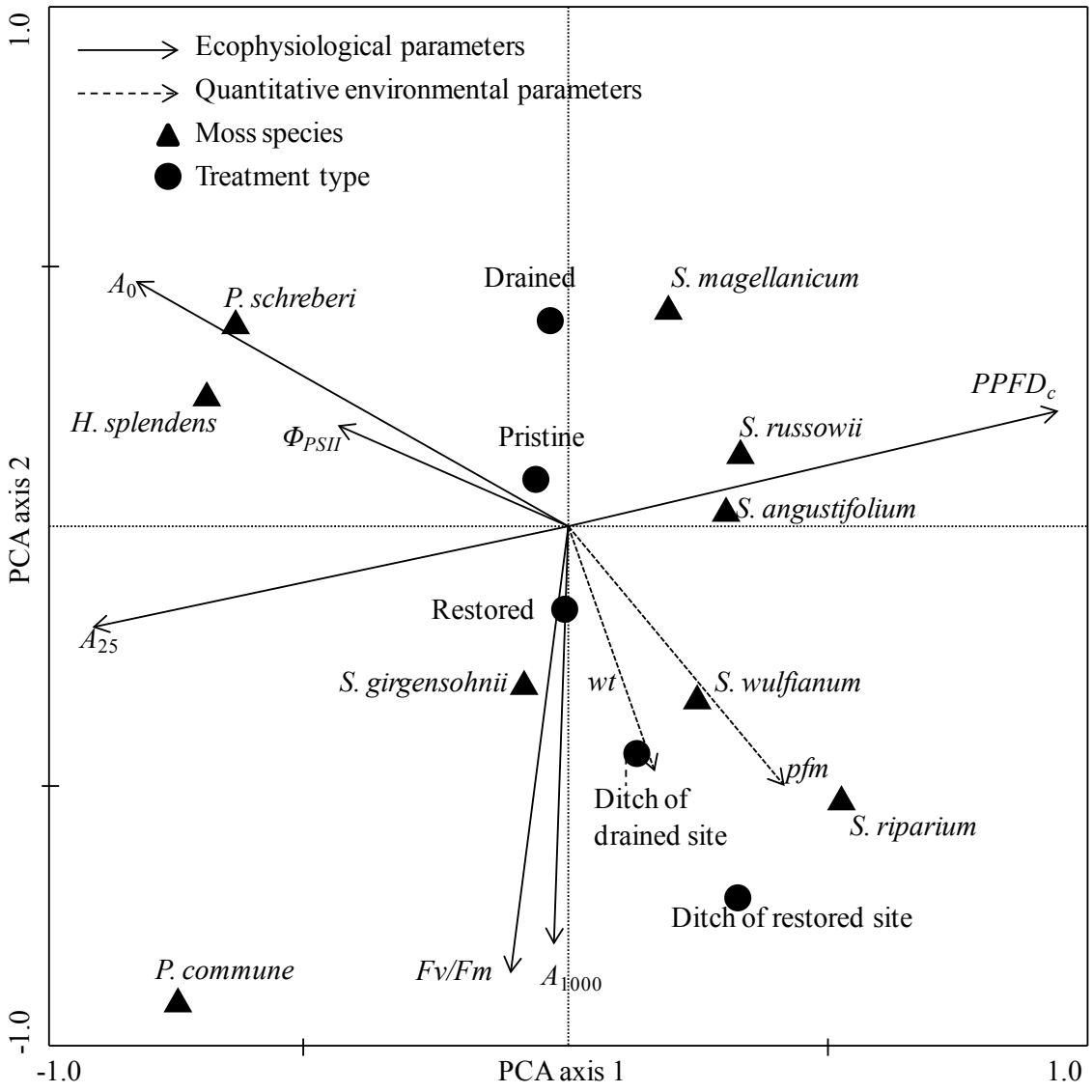

Figure 3.8 Principal Component Analysis (PCA) linking physiological response parameters (CO_2 assimilation rate at three levels of PPFD (A_{1000}, A_{25}, and A_0), light compensation point of A ($PPFD_c$), maximum quantum yield of PSII (F_v/F_m), and quantum yield of PSII (Φ_{PSII}) with environmental parameters (moss species, land use type, site water table (*wt*), and peat field moisture (*pfm*)) during May. Axes 1 and 2 explain 44% and 30% of total variation, respectively.

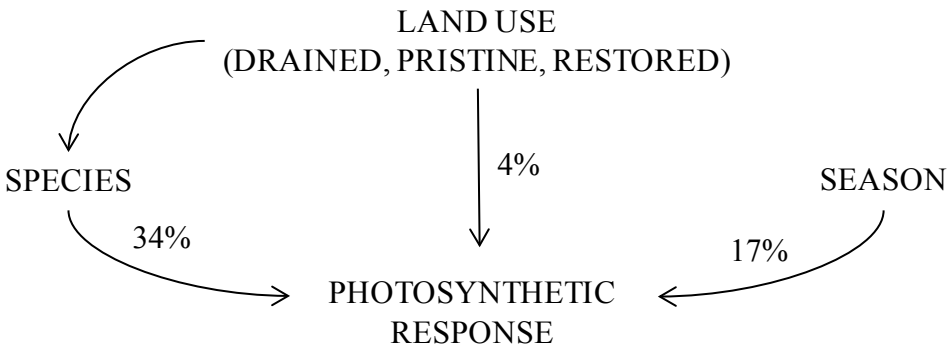

Figure 3.9 Diagram of direct and indirect land use effects on the photosynthetic responses of mire mosses. Values indicate the percentage of variation each factor directly explains.

4. Conclusion

The two chapters of this thesis address wetlands with different future trajectories and different methods used to initiate wetland conditions. There is a large difference between creating a wetland out of pre-existing upland versus rewetting drained peatlands. However, despite the differences present, the common link between all wetland creation/restoration activities is the importance of hydrology. Hydrology is an important factor controlling wetland processes, and plays a critical role in the functioning of the focal species groups in this thesis. As addressed in Chapter 1, microtopography, which played an important role in moderating water levels, was an important factor for northern white-cedar survival. In Chapter 2, differences in water levels were a key driver of species partitioning and therefore productivity.

A challenge regarding forested wetland restoration is the lengthy development period for focal vegetation communities, which makes it difficult to evaluate restoration methods in the short term. As a result, follow-up research will be needed in the future regarding both studies addressed here. As discussed in Chapter 1, northern white-cedar is a slow-growing tree and may take up to 40 years for seedlings to grow above deer browsing height (Van Deelen 1999), which clearly indicates the need for long-term monitoring of browsing impacts. In addition, although microtopography has been shown to be important in the short-term for northern white-cedar survival and the partitioning of understory vegetation communities, these relationships may change over time.

In Chapter 2, the evaluation of restored spruce swamp forests has occurred already 8–10 years after restoration. However, the current functioning of restored sites indicates that restored sites are still in the early stages of succession. The functioning of restored spruce swamp forests will likely change in the future as succession moves toward pristine conditions. The time period that this will take can only be determined by future studies.

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Appendix A

Table A.1
Average percent cover of herbaceous vegetation and bare soil by microtopography type in Petoskey. Total percent cover does not include bare soil.

Species	Wetland Indicator Status[+]	Native Status*	Hummock	Flat	Pool
Eleocharis palustris (L.) Roem. & Schult.	OBL	NATIVE	26.1	4.6	43.1
Alisma subcordatum Raf.	OBL	NATIVE*	0.01		27.5
Bare soil	na	na		17.3	17.4
Typha angustifolia L.	OBL	**INTRODUCED**	1.4	0.5	15.3
Juncus articulatus L.	OBL	NATIVE	3.8	6.4	8.6
Carex vulpinoidea Michx.	OBL	NATIVE*	29.4	5.6	5.5
Typha latifolia L.	OBL	NATIVE	0.4		5.2
Leersia oryzoides (L.) Sw.	OBL	NATIVE*	0.6	5.4	4.4
Carex lupulina Muhl. ex Willd.	OBL	NATIVE*	0.4	3.1	3.8
Scirpus atrovirens Willd.	OBL	NATIVE*	7.2	7.8	2.1
Carex bebbii Olney ex Fernald	OBL	NATIVE	3.3	0.5	1.8
Scirpus cyperinus (L.) Kunth	OBL	NATIVE	3.3	3.7	1.5
Carex retrorsa Schwein.	OBL	NATIVE	0.4	0.5	1.4
Lycopus uniflorus Michx.	OBL	NATIVE	0.03	0.01	0.9
Polygonum hydropiperoides Michx.	OBL	NATIVE		0.1	0.8
Agrostis stolonifera L.	FACW	**INTRODUCED**	26.7	34.4	0.7
Equisetum arvense L.	FAC	NATIVE	0.2	0.04	0.6
Bidens cernua L.	OBL	NATIVE*	0.01	0.3	0.5
Calamagrostis canadensis (Michx.) P. Beauv.	OBL	NATIVE*	2.0	0.1	0.5
Mimulus ringens L.	OBL	NATIVE*	0.4	0.3	0.2
Ambrosia artemisiifolia L.	FACU	NATIVE	0.01	3.4	0.1
Glyceria striata (Lam.) Hitchc.	OBL	NATIVE*	0.1		0.1
Carex hystericina Muhl. ex Willd.	OBL	NATIVE*			0.1
Rorippa palustris (L.) Besser	OBL	NATIVE	0.01		0.03
Prunella vulgaris L.	FAC	NATIVE	1.1	0.01	0.01
Plantago lanceolata L.	FAC	**INTRODUCED**	1.0	0.1	0.01
Phleum pratense L.	FACU	**INTRODUCED**	0.7	0.8	0.01
Carex granularis Muhl. ex Willd.	FACW+	NATIVE	4.8	0.4	0.01
Carex sp.	na	na	0.01	0.01	0.01

Table A.1 continued

Species	Wetland Indicator Status[+]	Native Status*	Hummock	Flat	Pool
unknown forb	na	na	0.04		0.01
Juncus tenuis Willd.	FAC	NATIVE	7.1	1.9	
Potentilla norvegica L.	FAC	NATIVE	0.03	0.0	
Rumex acetosella L.	FAC	**INTRODUCED**	0.03		
Erigeron annuus (L.) Pers.	FAC-	NATIVE	0.4		
Poa pratensis L.	FAC-	**INTRODUCED**	0.1		
Trifolium hybridum L.	FAC-	**INTRODUCED**	0.1	2.3	
Fragaria virginiana Duchesne	FAC-	NATIVE	0.01		
Elymus canadensis L.	FAC-	NATIVE*		0.0	
Plantago major L.	FAC+	**INTRODUCED**	0.2	0.1	
Rumex crispus L.	FAC+	**INTRODUCED**	0.1	0.0	
Panicum virgatum L.	FAC+	NATIVE*	0.01	11.2	
Hordeum jubatum L.	FAC+	NATIVE		0.01	
Elymus repens (L.) Gould	FACU	**INTRODUCED**	0.3	0.3	
Cerastium fontanum Baumg.	FACU	**INTRODUCED**	0.2		
Potentilla argentea L.	FACU	**INTRODUCED**	0.1		
Rudbeckia hirta L. var. pulcherrima Farw.	FACU	NATIVE	0.03		
Taraxacum officinale F.H. Wigg.	FACU	**INTRODUCED**	0.01	0.03	
Trifolium pratense L.	FACU+	**INTRODUCED**	0.01	0.1	
Veronica serpyllifolia L.	FACW	**INTRODUCED**	0.6		
Erigeron philadelphicus L.	FACW	NATIVE		0.0	
Juncus torreyi Coville	FACW	NATIVE		0.01	
Euthamia graminifolia (L.) Nutt. var. graminifolia	FACW-	NATIVE	1.5	0.5	
*Symphyotrichum lateriflorum (*L.) A. Löve & D. Löve *var. lateriflorum*	FACW-	NATIVE	0.5		
Ranunculus acris L.	FACW-	**INTRODUCED**	0.1	0.0	
Helenium autumnale L.	FACW+	NATIVE*		0.8	
Phalaris arundinacea L.	FACW+	NATIVE		0.1	
Grass sp.	na	na	2.3	1.1	
Barbarea sp.	na	na	0.2		
Oxalis sp.	na	na	0.2	0.1	
Salix sp.	na	na	0.1	0.0	
Bidens sp.	na	na		0.1	
Dicanthelium sp.	na	na		0.1	
Hypericum perforatum L.	not listed	**INTRODUCED**	21.3		

Table A.1 continued

Species	Wetland Indicator Status[+]	Native Status*	Hummock	Flat	Pool
Festuca saximontana Rydb.	not listed	NATIVE	0.3		
Potentilla recta L.	not listed	**INTRODUCED**	0.2		
Leucanthemum vulgare Lam.	not listed	**INTRODUCED**	0.2		
Trifolium campestre Schreb.	not listed	**INTRODUCED**		0.03	
Juncus effusus L.	OBL	NATIVE	2.2	0.1	
Scirpus pendulus Muhl.	OBL	NATIVE	0.2		
Juncus nodosus L.	OBL	NATIVE	0.1	0.3	
Carex stipata Muhl. ex Willd.	OBL	NATIVE	0.01		
Total Percent Cover			**152.2**	**97.1**	**124.6**

* Species planted

[+] A positive (+) or negative (-) sign more specifically defines the frequency of occurrence in wetlands within the given category: positive sign indicates more frequently found in wetlands, while a negative sign indicates less frequently found in wetlands.

Table A.2
Average percent cover of herbaceous vegetation and bare soil by microtopography type in Isabella.

Species	Wetland Indicator Status[+]	Native Status*	Hummock	Pool
Carex stipata Muhl. ex Willd.	OBL	NATIVE*	22.6	14.3
Lotus corniculatus L.	**FAC-**	**INTRODUCED**	33.0	14.0
Phalaris arundinacea L.	FACW+	**NATIVE**	34.4	12.7
Agrostis gigantea Roth	**FACW**	**INTRODUCED**	7.1	12.3
Carex granularis Muhl. ex Willd.	FACW+	NATIVE	3.4	8.8
Juncus dudleyi Wiegand	not listed	NATIVE	0.1	4.0
Plantago major L.	**FAC+**	**INTRODUCED**	1.9	4.0
Phleum pratense L.	**FACU**	**INTRODUCED**	2.3	1.9
Leucanthemum vulgare Lam.	not listed	**INTRODUCED**	10.1	1.9
Carex sp.	na	na		1.8
Asclepias incarnata L.	OBL	NATIVE*	0.0	1.5
Carex bebbii Olney ex Fernald	OBL	NATIVE*	1.1	1.3
Symphyotrichum puniceum (L.) A. Löve & D. Löve var. *puniceum*	OBL	NATIVE*	0.2	1.3
Carex vulpinoidea Michx.	OBL	NATIVE*	0.1	1.2
Salix sp.	na	na	0.1	1.2
Festuca saximontana Rydb.	not listed	NATIVE	1.9	1.0
Moss sp.	na	na	1.8	1.0
Juncus effusus L.	OBL	NATIVE*		1.0
Sisyrinchium montanum Greene	FAC+	NATIVE	1.8	0.6
Prunella vulgaris L.	FAC	NATIVE	0.4	0.4
Equisetum sp.	FAC	NATIVE	0.2	0.3
Potentilla norvegica L.	FAC	NATIVE	0.2	0.3
Trifolium pratense L.	**FACU+**	**INTRODUCED**	1.3	0.3
Taraxacum officinale F.H. Wigg.	**FACU**	**INTRODUCED**	0.5	0.3
Cicuta bulbifera L.	OBL	NATIVE	0.1	0.3
Hieracium sp.	na	na	1.0	0.2
Erigeron philadelphicus L.	FACW	NATIVE	0.4	0.2
Euthamia graminifolia (L.) Nutt. var. graminifolia	FACW-	NATIVE	0.2	0.2
Lycopus americanus Muhl. ex W. Bartram	OBL	NATIVE	0.1	0.2
Elymus canadensis L.	FAC-	NATIVE		0.2
Daucus carota L.	not listed	**INTRODUCED**	0.5	0.2
Hypericum perforatum L.	not listed	**INTRODUCED**	1.4	0.1
Eleocharis palustris (L.) Roem. & Schult.	OBL	NATIVE	0.3	0.1
Poa pratensis L.	**FAC-**	**INTRODUCED**	0.2	0.1
Dicanthelium sp.			0.1	0.1
Symphyotrichum lanceolatum (Willd.) G.L. Nesom	FACW	NATIVE	0.0	0.1

Table A.2 continued

Species	Wetland Indicator Status[+]	Native Status*	Hummock	Pool
Grass sp.	na	na		0.1
Juncus brevicaudatus (Engelm.) Fernald	OBL	NATIVE		0.1
Carex aurea Nutt.	FACW+	NATIVE	0.1	0.1
Elymus repens (L.) Gould	**FACU**	**INTRODUCED**	0.1	0.1
Fragaria virginiana Duchesne	FAC-	NATIVE	0.1	0.1
Fraxinus pennsylvanica Marsh.	FACW	NATIVE	0.1	0.1
Ranunculus acris L.	**FACW-**	**INTRODUCED**	0.1	0.1
Symphyotrichum lateriflorum (L.) A. Löve & D. Löve var. *lateriflorum*	FACW-	NATIVE	0.0	0.1
Galium palustre L.	not listed	NATIVE	0.0	0.1
Plantago lanceolata L.	**FAC**	**INTRODUCED**	0.4	0.1
Trifolium hybridum L.	**FAC-**	**INTRODUCED**		0.1
Solidago rugosa Mill.	FAC+	NATIVE	0.2	0.03
Viola sp.	na	na	0.1	0.03
Argentina anserina (L.) Rydb.	FACW+	NATIVE	0.03	0.03
Carex retrorsa Schwein.	OBL	NATIVE		0.03
Eupatoriadelphus maculatus (L.) King & H. Rob. var. *maculatus*	OBL	NATIVE*		0.03
Glyceria striata (Lam.) Hitchc.	OBL	NATIVE*		0.03
Juncus articulatus L.	OBL	NATIVE		0.03
Juncus torreyi Coville	FACW	NATIVE		0.03
Ulmus americana L.	FACW-	NATIVE		0.03
unknown forb	na	na		0.03
Solidago altissima L.	FACU	NATIVE	1.0	
Erigeron annuus (L.) Pers.	FAC-	NATIVE	0.3	
Cirsium vulgare (Savi) Ten.	**FACU-**	**INTRODUCED**	0.1	
Juncus nodosus L.	OBL	NATIVE	0.1	
Clinopodium vulgare L.	not listed	NATIVE	0.1	
Ambrosia artemisiifolia L.	FACU	NATIVE	0.03	
Carex gracillima Schwein.	FACU	NATIVE	0.03	
Festuca sp.	na	na	0.03	
Geum sp.	na	na	0.03	
Rubus idaeus L.	**FACU+**	**INTRODUCED**	0.03	
Solidago gigantea Aiton	FACW	NATIVE	0.03	
Total Percent Cover			**131.5**	**90.7**

* Species planted

[+] A positive (+) or negative (-) sign more specifically defines the frequency of occurrence in wetlands within the given category: positive sign indicates more frequently found in wetlands, while a negative sign indicates less frequently found in wetlands.

Appendix B

Table B.1
Species measured by site and treatment type.

Pristine	Drained	Restored
Site	Site	Site
Species	*Species*	*Species*
EvLuVK	**LakkOj**	**Ev03ku**
Pleurozium schreberi	**Ditch**	**Ditch**
*S. angustifolium**	*S. magellanicum**	*S. girgensohnii*[1]
S. girgensohnii	**Main site**	*S. riparium*
S. magellanicum	*Pleurozium schreberi*	**Main site**
S. wulfianum	*S. girgensohnii*	*Hylocomium splendens**
	S. magellanicum	*Pleurozium schreberi*
	*S. russowii**	*S. angustifolium**
		*S. russowii**
SusiLu	**KoniOj**	**Ev03ma**
Pleurozium schreberi	**Main site**	**Ditch**
*S. angustifolium**	*Pleurozium schreberi*	*S. riparium*
S. girgensohnii	*S. angustifolium**	*S. russowii*
*S. magellanicum**	*S. girgensohnii*	**Main site**
S. riparium	*S. magellanicum*	*Pleurozium schreberi*
S. russowii	*S. russowii**	*S. angustifolium**
		S. girgensohnii
		*S. wulfianum**
EvLuPa	**VesiOj**	**Ev01VR**
Pleurozium schreberi	**Ditch**	**Ditch**
*Polytrichum commune**	*S. riparium*	*S. riparium*
*S. angustifolium**	*S. girgensohnii*[2]	**Main site**
S. girgensohnii	**Main site**	*Pleurozium schreberi*
S. magellanicum	*Pleurozium schreberi*	*S. angustifolium**
	*Hylocomium splendens**	*S. girgensohnii*
		*S. russowii**
		*S. wulfianum**

* Sampled only during May measurement period

[1] Sampled near ditch in May, in ditch remaining months (limited coverage of *S.girgensohnii* outside of ditch)

[2] Sampled in ditch in May, in main site in remaining months

Table B.2

Net photosynthesis rate at $PPFD_{1000\ \mu mol\ m-2s-1}$ (A_{1000}) for species measured during all four sampling periods across treatment type and month. Means ± SE.

A_{1000} (mg g-1 h-1)	May	June	July	August
Pleurozium schreberi				
Drained, main site	3.2 ± 0.26	4.0 ± 0.34	3.2 ± 0.40	3.6 ± 0.39
Pristine	3.1 ± 0.35	2.9 ± 0.16	3.5 ± 0.38	3.9 ± 0.39
Restored, main site	3.1 ± 0.21	4.0 ± 0.35	3.7 ± 0.24	4.4 ± 0.38
S. girgensohnii				
Drained, ditch	5.8 ± 0.97			
Drained, main site	3.6 ± 0.55	5.2 ± 0.71	4.8 ± 0.40	5.2 ± 0.33
Pristine	4.3 ± 0.39	5.0 ± 0.26	5.5 ± 0.34	4.9 ± 0.40
Restored, ditch		4.2 ± 0.52	6.7 ± 0.65	4.8 ± 0.12
Restored, main site	4.6 ± 0.67	6.5 ± 0.48	7.3 ± 0.74	6.4 ± 0.50
S. magellanicum				
Drained, main site	2.8 ± 0.48	5.0 ± 0.30	3.7 ± 0.75	3.9 ± 0.62
Pristine	2.9 ± 0.29	4.0 ± 0.37	4.7 ± 0.65	4.2 ± 0.28
S. riparium				
Drained, ditch	6.4 ± 1.99	8.5 ± 0.67	7.4 ± 0.73	4.1 ± 0.45
Pristine	3.9 ± 0.20	5.7 ± 1.11	6.0 ± 0.33	3.3 ± 0.42
Restored, ditch	7.1 ± 0.44	8.2 ± 0.75	7.3 ± 0.56	5.6 ± 0.58
S. russowii				
Pristine	2.0 ± 0.18	3.5 ± 1.02	4.9 ± 0.67	4.8 ± 0.76
Restored, ditch	5.1 ± 0.55	6.4 ± 0.74	6.9 ± 1.62	3.4 ± 0.88
S. wulfianum				
Pristine	2.8 ± 0.26	2.3 ± 0.31	2.6 ± 0.33	3.0 ± 0.06

Table B.3
Dark respiration rate (A_0) for species measured during all four sampling periods across treatment type and month. Means ± SE.

A_0 (mg g-1 h-1)	May	June	July	August
Pleurozium schreberi				
Drained, main site	-0.90 ± 0.08	-0.38 ± 0.08	-0.64 ± 0.06	-0.68 ± 0.06
Pristine	-0.75 ± 0.08	-0.50 ± 0.04	-0.29 ± 0.05	-0.30 ± 0.02
Restored, main site	-0.75 ± 0.06	-0.40 ± 0.08	-0.51 ± 0.09	-0.40 ± 0.03
S. girgensohnii				
Drained, ditch	-1.18 ± 0.10			
Drained, main site	-1.62 ± 0.13	-0.86 ± 0.07	-1.03 ± 0.08	-1.15 ± 0.08
Pristine	-1.51 ± 0.11	-1.14 ± 0.06	-0.96 ± 0.09	-0.91 ± 0.05
Restored, ditch		-0.86 ± 0.11	-0.96 ± 0.10	-0.96 ± 0.07
Restored, main site	-1.67 ± 0.11	-1.23 ± 0.09	-0.99 ± 0.07	-1.09 ± 0.09
S. magellanicum				
Drained, main site	-1.32 ± 0.12	-1.07 ± 0.07	-1.16 ± 0.08	-1.09 ± 0.09
Pristine	-1.49 ± 0.14	-1.23 ± 0.04	-0.75 ± 0.12	-0.91 ± 0.04
S. riparium				
Drained, ditch	-2.15 ± 0.07	-0.85 ± 0.04	-1.11 ± 0.24	-1.35 ± 0.13
Pristine	-1.92 ± 0.17	-1.51 ± 0.06	-1.24 ± 0.06	-1.54 ± 0.27
Restored, ditch	-2.12 ± 0.13	-1.52 ± 0.09	-1.62 ± 0.13	-1.81 ± 0.16
S. russowii				
Pristine	-1.64 ± 0.10	-1.33 ± 0.08	-1.40 ± 0.23	-1.17 ± 0.17
Restored, ditch	-1.76 ± 0.26	-1.09 ± 0.04	-0.96 ± 0.02	-1.19 ± 0.09
S. wulfianum				
Pristine	-1.55 ± 0.24	-1.81 ± 0.16	-1.24 ± 0.13	-1.02 ± 0.13

Table B.4
Light compensation point ($PPFD_c$) for species measured during all four sampling periods across treatment type and month. Means ± SE.

$PPFD_c$	May	June	July	August
Pleurozium schreberi				
Drained, main site	20.1 ± 1.71	10.2 ± 1.27	14.4 ± 1.19	15.1 ± 1.33
Pristine	18.6 ± 2.21	13.3 ± 1.07	8.7 ± 1.15	9.0 ± 0.40
Restored, main site	21.3 ± 2.11	11.7 ± 1.77	11.9 ± 1.40	10.3 ± 0.50
S. girgensohnii				
Drained, ditch	18.7 ± 1.40			
Drained, main site	30.3 ± 2.69	14.9 ± 1.46	16.2 ± 0.82	18.5 ± 1.28
Pristine	25.4 ± 1.55	18.5 ± 1.35	14.3 ± 1.66	15.7 ± 1.19
Restored, ditch		14.5 ± 1.83	13.8 ± 1.83	15.8 ± 0.94
Restored, main site	26.9 ± 1.13	18.4 ± 1.67	16.5 ± 2.77	15.6 ± 1.27
S. magellanicum				
Drained, main site	34.6 ± 3.16	19.8 ± 1.40	25.5 ± 4.79	23.2 ± 2.74
Pristine	33.7 ± 4.07	22.8 ± 1.23	13.0 ± 2.72	17.9 ± 1.13
S. riparium				
Drained, ditch	39.4 ± 7.03	13.3 ± 0.63	16.5 ± 3.98	27.5 ± 1.87
Pristine	36.9 ± 5.92	30.0 ± 1.73	22.3 ± 1.85	29.8 ± 4.55
Restored, ditch	32.4 ± 3.74	22.4 ± 1.48	27.2 ± 2.34	28.3 ± 2.29
S. russowii				
Pristine	38.6 ± 3.32	28.8 ± 5.70	23.2 ± 3.64	20.1 ± 3.62
Restored, ditch	30.6 ± 4.41	17.3 ± 1.11	18.0 ± 5.12	25.3 ± 5.70
S. wulfianum				
Pristine	30.3 ± 1.71	36.0 ± 3.29	23.2 ± 3.60	18.9 ± 2.44

Table B.5
Maximum quantum yield of PSII photochemistry (F_v/F_m) for species measured during all four sampling periods across treatment type and month. Means ± SE.

F_v/F_m	May	June	July	August
Pleurozium schreberi				
Drained, main site	0.70 ± 0.009	0.74 ± 0.004	0.74 ± 0.01	0.77 ± 0.007
Pristine	0.72 ± 0.006	0.74 ± 0.003	0.74 ± 0.01	0.77 ± 0.004
Restored, main site	0.71 ± 0.012	0.74 ± 0.008	0.75 ± 0.01	0.78 ± 0.004
S. girgensohnii				
Drained, ditch	0.75 ± 0.011			
Drained, main site	0.73 ± 0.007	0.76 ± 0.009	0.72 ± 0.01	0.78 ± 0.005
Pristine	0.74 ± 0.012	0.78 ± 0.005	0.77 ± 0.01	0.78 ± 0.003
Restored, ditch		0.77 ± 0.011	0.76 ± 0.01	0.79 ± 0.013
Restored, main site	0.75 ± 0.008	0.78 ± 0.003	0.77 ± 0.02	0.81 ± 0.004
S. magellanicum				
Drained, main site	0.65 ± 0.017	0.75 ± 0.006	0.70 ± 0.01	0.75 ± 0.008
Pristine	0.70 ± 0.012	0.75 ± 0.005	0.76 ± 0.00	0.76 ± 0.003
S. riparium				
Drained, ditch	0.74 ± 0.019	0.78 ± 0.009	0.72 ± 0.01	0.76 ± 0.014
Pristine	0.70 ± 0.031	0.75 ± 0.006	0.65 ± 0.03	0.76 ± 0.004
Restored, ditch	0.75 ± 0.009	0.77 ± 0.006	0.72 ± 0.01	0.77 ± 0.007
S. russowii				
Pristine	0.73 ± 0.019	0.77 ± 0.012	0.72 ± 0.00	0.79 ± 0.004
Restored, ditch	0.77 ± 0.007	0.79 ± 0.008	0.75 ± 0.03	0.80 ± 0.012
S. wulfianum				
Pristine	0.75 ± 0.022	0.76 ± 0.006	0.78 ± 0.01	0.79 ± 0.002

Table B.6
Quantum yield of PSII photochemistry (Φ_{PSII}) for species measured during all four sampling periods across treatment type and month. Means ± SE.

Φ_{PSII}	May	June	July	August
Pleurozium schreberi				
Drained, main site	0.195 ± 0.013	0.185 ± 0.008	0.128 ± 0.009	0.170 ± 0.019
Pristine	0.217 ± 0.024	0.169 ± 0.013	0.157 ± 0.019	0.186 ± 0.012
Restored, main site	0.186 ± 0.020	0.210 ± 0.019	0.144 ± 0.016	0.204 ± 0.021
S. girgensohnii				
Drained, ditch	0.095 ± 0.009			
Drained, main site	0.107 ± 0.012	0.086 ± 0.002	0.078 ± 0.005	0.091 ± 0.005
Pristine	0.107 ± 0.005	0.088 ± 0.005	0.094 ± 0.004	0.093 ± 0.005
Restored, ditch		0.071 ± 0.006	0.083 ± 0.006	0.090 ± 0.005
Restored, main site	0.118 ± 0.005	0.096 ± 0.006	0.092 ± 0.010	0.116 ± 0.005
S. magellanicum				
Drained, main site	0.119 ± 0.008	0.077 ± 0.005	0.076 ± 0.004	0.102 ± 0.005
Pristine	0.108 ± 0.007	0.087 ± 0.003	0.087 ± 0.005	0.093 ± 0.006
S. riparium				
Drained, ditch	0.111 ± 0.013	0.077 ± 0.007	0.067 ± 0.004	0.069 ± 0.008
Pristine	0.106 ± 0.012	0.077 ± 0.009	0.086 ± 0.024	0.114 ± 0.011
Restored, ditch	0.143 ± 0.005	0.103 ± 0.004	0.091 ± 0.005	0.105 ± 0.008
S. russowii				
Pristine	0.120 ± 0.006	0.106 ± 0.007	0.091 ± 0.004	0.113 ± 0.005
Restored, ditch	0.163 ± 0.005	0.107 ± 0.006	0.088 ± 0.016	0.130 ± 0.025
S. wulfianum				
Pristine	0.153 ± 0.017	0.123 ± 0.003	0.112 ± 0.010	0.116 ± 0.005

Table B.7
Photosynthetic response parameters for all species during the month of May according to treatment type. Means ± SE.

Species Treatment	A_{1000} (mg g-1 h-1)	A_0 (mg g-1 h-1)	$PPFD_c$ (µmol $m^{-2}s^{-1}$)	F_v/F_m	Φ_{PSII}
Hylocomium splendens					
Drained, main site	3.28 ± 0.39	-1.08 ± 0.15	20.3 ± 2.20	0.71 ± 0.007	0.17 ± 0.019
Restored, main site	3.28 ± 0.44	-0.61 ± 0.04	13.8 ± 0.38	0.73 ± 0.006	0.18 ± 0.010
Pleurozium schreberi					
Drained, main site	3.22 ± 0.26	-0.90 ± 0.08	20.1 ± 1.71	0.70 ± 0.009	0.20 ± 0.013
Pristine	3.05 ± 0.35	-0.75 ± 0.08	18.6 ± 2.21	0.72 ± 0.006	0.22 ± 0.024
Restored, main site	3.08 ± 0.21	-0.75 ± 0.06	21.3 ± 2.11	0.71 ± 0.012	0.19 ± 0.020
Polytrichum commune					
Pristine	6.92 ± 1.00	-0.88 ± 0.07	17.8 ± 0.44	0.81 ± 0.010	0.18 ± 0.012
S. angustifolium					
Drained, main site	2.12 ± 0.15	-1.48 ± 0.09	37.2 ± 1.22	0.68 ± 0.008	0.15 ± 0.024
Pristine	2.75 ± 0.14	-1.61 ± 0.07	34.4 ± 1.68	0.72 ± 0.011	0.13 ± 0.007
Restored, main site	4.71 ± 0.65	-1.92 ± 0.16	32.4 ± 2.19	0.76 ± 0.004	0.13 ± 0.011
S. girgensohnii					
Drained, ditch	5.83 ± 0.97	-1.18 ± 0.10	18.7 ± 1.40	0.75 ± 0.011	0.09 ± 0.009
Drained, main site	3.61 ± 0.55	-1.62 ± 0.13	30.3 ± 2.69	0.73 ± 0.007	0.11 ± 0.012
Pristine	4.28 ± 0.39	-1.51 ± 0.11	25.4 ± 1.55	0.74 ± 0.012	0.11 ± 0.005
Restored, main site	4.64 ± 0.67	-1.67 ± 0.11	26.9 ± 1.13	0.75 ± 0.008	0.12 ± 0.005
S. magellanicum			2.22		
Drained, ditch	3.81 ± 0.38	-1.76 ± 0.15	29.0 ± 1.35	0.72 ± 0.012	0.10 ± 0.009
Drained, main site	2.78 ± 0.48	-1.32 ± 0.12	34.6 ± 3.16	0.65 ± 0.017	0.12 ± 0.008
Pristine	2.84 ± 0.28	-1.37 ± 0.12	32.6 ± 3.96	0.70 ± 0.011	0.10 ± 0.006
S. riparium					
Drained, ditch	6.40 ± 1.99	-2.15 ± 0.07	39.4 ± 7.03	0.74 ± 0.019	0.11 ± 0.013
Pristine	3.85 ± 0.20	-1.92 ± 0.17	36.9 ± 5.92	0.70 ± 0.031	0.11 ± 0.012
Restored, ditch	7.13 ± 0.44	-2.12 ± 0.13	32.4 ± 3.74	0.75 ± 0.009	0.14 ± 0.005

Table B.7 continued
Photosynthetic response parameters for all species during the month of May according to treatment type. Means ± SE.

Species Treatment	A_{1000} (mg g-1 h-1)	A_0 (mg g-1 h-1)	$PPFD_c$ (µmol $m^{-2}s^{-1}$)	F_v/F_m	Φ_{PSII}
S. russowii					
Drained, main site	2.15 ± 0.39	-1.45 ± 0.07	37.3 ± 5.00	0.71 ± 0.014	0.13 ± 0.006
Pristine	1.98 ± 0.18	-1.64 ± 0.10	38.6 ± 3.32	0.73 ± 0.019	0.12 ± 0.006
Restored, ditch	4.25 ± 0.62	-1.77 ± 0.18	32.9 ± 2.53	0.76 ± 0.004	0.16 ± 0.013
Restored, main site	2.64 ± 0.94	-1.49 ± 0.13	35.2 ± 3.60	0.74 ± 0.025	0.13 ± 0.011
S. wulfianum					
Pristine	2.78 ± 0.26	-1.55 ± 0.24	30.3 ± 1.71	0.75 ± 0.022	0.15 ± 0.017
Restored, main site	3.88 ± 0.53	-2.23 ± 0.27	33.4 ± 2.29	0.78 ± 0.005	0.13 ± 0.006